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THE VEGETATION OF THE INLAND SAND DEPOSITS OF ILLINOIS

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ARTICLE III.—*The Vegetation of the Inland Sand Deposits of Illinois.* By HENRY ALLAN GLEASON.

INTRODUCTION*

In the rapid development of ecological and phytogeographical knowledge during the past few decades, the vegetation of sand deposits has been the subject of especially frequent and detailed study. At least three reasons may be mentioned why this type of vegetation has received particular attention. First, sand deposits are usually well developed and form dune complexes of greater or less extent along the shores of the ocean or the larger inland lakes, and in many cases are convenient places for vacation trips. Secondly, the vegetation on sand is usually open and easily studied, and the dynamic nature of the environment is emphasized. For this reason the interrelations of plant and environment are more easily observed and offer attractive fields for study. Thirdly, sand areas are usually infertile in comparison with their surroundings. They are accordingly frequently left uncultivated and constitute temporary natural preserves, in which the original types of vegetation persist and are available for study.

In the case of the inland sand regions of Illinois the first statement is hardly effective, and that may explain why they have received relatively little attention from local botanists. At the present time, however, they comprise the largest, and virtually the only, areas of natural vegetation within the state. With the exception of parts of the sand deposits, of some small swamp areas, of rock outcrops, of ponds and lakes, and of some small tracts of forest, all the original vegetation of Illinois has been destroyed or greatly modified by clearing, planting, or pasturing. The area covered by the last four of these exceptions is very small, but there are still thousands of acres of sand deposits in nearly original condition and available for study They still contain some virgin prairie that has never been plowed or pastured. These prairies are probably somewhat different from the more representative types of prairie which formerly grew upon more fertile soil, but they are much more nearly typical than the small strips still occurring along the margins of some streams and ponds.

* The field work upon which this article is based, was carried on by the aid of a grant from the Botanical Society of America. Further financial assistance was given by the Illinois State Laboratory of Natural History.

The study of the vegetation of the sand deposits of Illinois is therefore of especial scientific interest because they constitute the only considerable area of natural vegetation in the state, and because their vegetation is closely related to that of the original prairie. It is also of some general value, since it concerns an area which has received little attention from botanists, and because it affords intelligible illustrations of certain ecological principles.

The field work upon which the present paper is based was done during the summer of 1908. Reference is also frequently made to the field work at Havana in August, 1903, and August, 1904, the results of which have already been published (Hart and Gleason, *1907*). The itinerary during 1908 was as follows:

May 28, 29, St. Anne, Kankakee county.

May 31-June 3, June 12-24, August 15-18, Hanover, Jo Daviess county.

June 25-29, Shirland, Winnebago county.

June 30-July 3, August 19, 20, Dixon, Lee county.

July 4-15, August 10-14, Oquawka, Henderson county.

July 16, Forest City, Mason county.

August 7, Topeka, Mason county.

August 8, Havana, Mason county.

August 21, Amboy, Lee county.

From June 12 to 19 Mr. Frank C. Gates assisted in the field work. He also identified many of the plants mentioned in the paper. The grasses and sedges were identified through the courtesy of Mrs. Agnes Chase. Mr. H. N. Patterson rendered important assistance in the field work in the Oquawka area. Dr. H. S. Pepoon has supplied valuable information concerning the Hanover area. To each of these the writer extends his thanks for their interest and appreciation.

The photographs have been taken by the writer, using a folding film camera, Ansco films, and tank development.

Physiography and Origin

The chief sand deposits of Illinois lie in the northern half of the state, between latitude 40° and 42° 30′. In the southern half sand occurs only in small local deposits or in bars near the larger rivers, and is never of such extent that a peculiar vegetation is developed upon it. Banks and bars of sand also border the streams of northern Illinois, but their vegetation bears little relation to that of the larger deposits here described.

For convenience the sand areas have been given names taken from

some geographical feature of the vicinity. Some of these areas are contiguous, and some owe their existence to the same causes. The names, therefore, do not indicate areas which are geologically distinct, but merely general locations in which the field work was prosecuted. The geography of each of these regions will be described separately.

The Havana Area.—The Tazewell sheet of the Field Operations of the Bureau of Soils (Bonsteel, *1903a*) shows the northern extremity of this deposit, and illustrates its relation to the glacial valley of the Illinois river. North of Pekin, in Tazewell county, the Illinois river cuts through the Shelbyville and Bloomington moraines, flowing close to high bluffs on its left (eastern) side. From this point southward the river crosses the broad glacial valley diagonally toward the right, exposing a triangular area of lowland between the channel and the east bluffs. The sand is deposited in this glacial flood-plain. At Pekin the plain is about two miles (3 km.) wide; below that city it widens more abruptly, and near Green Valley is 14 miles (22 km.) wide. At some places near the river the plain is covered with modern alluvial deposits, and it is crossed by the Mackinaw river with its broad flood-plain. The remaining area is occupied by sand and by a sandy loam, shown in the Soil Survey as Miami sandy loam. The latter lies at a lower level and represents the original alluvial deposits upon which the sand has been superposed. In this county 22,976 acres (90 sq. km.) are covered with sand. South of Tazewell county the plain retains its maximum width across Mason county, and then becomes gradually narrower toward the south, terminating near Meredosia, Morgan county, with a total length of approximately 75 miles (120 km.). While sand deposits occupy only a portion of this area, their aggregate extent is large and has been estimated (Hart and Gleason, *1907:* 145, 146) at 179,200 acres (700 sq. km.).

The Chicago, Peoria and St. Louis railway traverses the areas from Peoria through Havana to Virginia, and a good idea of the general topography may be gained from its trains. The exposed areas of Miami sandy loam, which forms the foundation of the whole, are irregular in shape and extremely variable in size, ranging from a few acres up to several square miles. They are almost entirely under cultivation. Above them rise the low sand hills (Pl. I, Fig. 1), usually gently undulating at their margins but, if large in extent, frequently quite level toward the center. These vary in size from mere hills of a few acres up to continuous deposits several miles in extent. Their average height is probably 20-30 feet (6-10 m.), but isolated

dunes rise much higher. One of the highest lies about four miles (6 km.) north of Topeka, and is probably about 60 feet (18 m.) above the general level. Part of the sand was originally covered with prairie, but most of this has been destroyed by cultivation and pasturing, so that only a few small areas remain in their natural condition. A larger portion has been forested, and much of it remains in its virgin state. Particularly large tracts of forest are situated near Forest City and between Kilbourne and Bath.

The Hanover Area.—This region of sand deposition takes its name from the station of the Chicago, Burlington and Quincy railway in Jo Daviess county, which lies near the location of the best development of sand vegetation. As in the Havana area the sand occupies the so-called second bottom, between the bluffs on the east and the Mississippi river on the west. In some places the sand extends to the river's edge, in others a strip of alluvial forested floodplain intervenes. In the northern portion of the county the bluffs lie close to the river and the sand is limited to small isolated areas. In the southern half the bluffs and river become one to three miles (2-5 km.) apart, affording space for an extensive sand deposit. North of Savanna, in Carroll county, the river again flows directly at the base of the bluffs. The area in Jo Daviess county covered by sand is estimated at 5700 acres (22 sq. km.).

Unlike the Havana area, the sand deposits here are nearly continuous and unbroken by intervening areas of a different soil. The surface of the area is gently rolling, with virtually no extensive level tracts. Its general elevation is about 25 feet (8 m.) above the river, but isolated dunes reach a much greater height. Near the eastern margin of the valley the depth of sand abruptly decreases, leaving a trough-like valley extending for a long distance at the base of the bluffs. The Chicago, Burlington and Quincy railway lies mainly in this depression. The drainage from the hills enters the valley through a number of small spring-fed streams. None of these has sufficient energy to erode a valley through the sand, and their discharge merely accumulates in a series of swamps, which are drained by percolation through the sand into the river beyond. The swamps are not continuous, but are separated by tracts of moist ground, originally prairie (the lower prairie of Pepoon, *1909:* 526) but now almost entirely under cultivation.

The sand deposit is chiefly prairie, but a belt of forest lies along the river, and tongues and irregular areas of forest project out into the prairie, in some places extending nearly across. Some of the forest and most of the prairie have been placed under cultivation, but

extensive areas of each are still in their original condition, or but slightly modified by pasturing.

Below Savanna, sand deposits of the same age again appear and continue intermittently down the Mississippi into Rock Island county, where they connect with those of the Oquawka area described later.

The geological origin of these two sand areas is known with considerable accuracy. Both are approximately contemporaneous and are derived from outwash from the Wisconsin glaciers. The method of deposition has been well described by Chamberlin and Salisbury (*1885:* 261, 262), with special reference to the Hanover area.

"*The fringing deposits of glacial waters.*—Outside the moraine lie two classes of deposits which gathered apace with it. The precipitation which fell upon the western slope of the glacial lobe, together with the water which arose from the same part of the glacier by melting, was shed from the edge, except the portion which may have found exit beneath in other directions and the portion lost by evaporation. Copious streams were doubtless the result. It is not difficult to understand that these, as they issued from the glacier, should have been exceptionally charged with silt, sand, and rolling stone, and that, as turbid waters, they poured down the channel-ways that were open to them. Long trains of glacial wash stretching away from the edge of the ice and leading down the several valleys testify to the reality of such streams.

"The most notable flood-train originating on the actual border of the driftless region is that which stretches down the valley of the Wisconsin River. The edge of the ice lobe crossed the Wisconsin in the western part of Dane and Sauk counties. In the immediate valley of the river the moraine is largely composed of gravelly constituents, disposed in kame-like hills and ridges, or undulatory and pitted plains, showing the combined action of wash and push on the part of the glacier and its waters. Originating from this gravelly moraine, there stretches away a flood-train of gravel and sand, reaching down the valley to the Mississippi, and, there joining similar gravel streams originating higher up, it continues down through the driftless area and beyond, though only remnants now remain. This valley drift originates at a height of about 90 feet above the present level of the Wisconsin River, and as it stretches down the valley gradually declines, so that, as it leaves the driftless region, it is barely 50 feet above the Mississippi. Near its origin coarse cobbles, bowlderets, and even occasional bowlders are not infrequent. Farther down, the material becomes finer, and, in the lower stretches, only pebbles and sand are found. The lessening coarseness of the deposit

seems to show that as the glacial waters issued from the edge of the ice they were overloaded and struggling with a burden too great for their complete mastery; and, while they successfully carried the silt, sand, and even some of the finer gravel far down their courses, the heavier material in large part lodged near its origin and progressively filled the bottom of the channel.

"This phenomenon, of which the Wisconsin Valley presents the only complete example lying entirely within the driftless region, finds other examples in several streams which cross the region. The Black River, the Chippewa, the Mississippi, and the Zumbro are all attended by such glacial flood deposits, which may be traced back to their origin on the face of the outer moraine. All these glacial flood plains slope more rapidly than the present streams. The train in the Chippewa Valley falls a little more than six feet per mile in the first 40 miles of its course, and over five feet per mile from its source on the face of the moraine to the Mississippi. In crossing the driftless area the glacial flood plain of the Mississippi declines about 50 feet more than the present stream."

Their description applies as well to the sands of the Havana area, except that the source of the latter is the outwash through the Bloomington moraine in the vicinity, as already described by Hart (Hart and Gleason, *1907:* 139-144).

The Amboy Area.—This name is given in this report to the irregular complex of sand ridges and marshes along the Green river in Lee county, well illustrated in the vicinity of Amboy. Near that place the sand occupies a strip about four miles (6 km.) wide on the south (left) bank of the river. It lies usually in comparatively narrow ridges from 20-50 feet (6-15 m.) above the intervening marshes. Back from the river the ridges are broader and the marshes proportionately more limited in size. Numerous small undrained ponds and swamps lie among the ridges. Near Amboy the ridges are either forested or under cultivation, but the number of prairie species occupying the roadsides indicates that at least a portion of the sand was originally covered with prairie.

Alternating areas of swamp and sand border Green river along its whole course through Lee, Bureau, and Henry counties to its junction with Rock river, a distance of about 70 miles (110 km.). They are to be regarded as outwash from the Bloomington morainal system, which crosses the south part of Lee county from northeast to southwest (Leverett, *1899:* 277, 492, 493). The drainage of the whole valley is poor, and two large marsh areas, known as the Inlet Swamp and the Winnebago Swamp, are as yet not entirely reclaimed.

Probably the present local swamps are the vestiges of large continuous marshes which formerly extended the whole length of the river, and the hydrophytic plant associations now between the dunes are doubtless the survivors of an earlier swamp vegetation. Slow drainage has permitted the formation of extensive muck deposits, while in the Illinois river valley more rapid and complete drainage has merely left areas of a sandy loam between the dunes.

The Dixon Area.—A small outlier of this general area, situated four miles (6 km.) southwest of the city of Dixon, is referred to under this name in the subsequent pages. This area is not forested, but the small marshes among the dunes indicate by their vegetation a close similarity to the rest of the area.

The Oquawka Area.—Below the mouth of Rock river the Mississippi turns sharply to the south and follows a generally southerly direction for about 60 miles (100 km.). Through this portion of its course, from Muscatine, Iowa, to Ft. Madison, Iowa, its valley is well filled with sand deposits. These are probably chiefly a continuation of those along Green river, derived from outwash from the Bloomington moraine. It is possible that some of the sand is derived from the Wisconsin river outwash, as described above under the Hanover area.

At the northern end of this area the principal deposits lie on the Iowa side of the river, where their vegetation has been briefly described by Pammel (*1899*). In Illinois the sand extends in a strip through the western part of Mercer and Henderson counties, lying usually close to the river, and gradually becoming thinner and less nearly continuous toward the south. A branch of the Chicago, Burlington and Quincy railway crosses the deposits between Aledo and New Boston and follows them south from Arpee to the junction with the main line at Gladstone. The town of Oquawka is situated on the deposits, and is a convenient location for the study of the sand vegetation.

At the north end of Henderson county the sand lies in large, continuous, nearly level areas, with here and there at wide intervals a low ridge. Its general height is 30-50 feet (10-15 m.) above the river. The ridges rise a few feet higher and near the Mississippi the river dune reaches a maximum height of about 100 feet (30 m.). Toward the south the sand lies in irregular, gently rolling ridges, not more than 30 feet (9 m.) high, and separated by areas of a sandy loam. South of Oquawka the deposits are broken by the Henderson river, but beyond it low ridges reappear and continue to the southern edge of the county.

A large proportion of the area has been forested, and most of that part is not under cultivation. Some fields have been cleared and abandoned, and are now densely covered with a thick growth of small trees. The portion originally covered with prairie is almost entirely under cultivation. Some large areas of blowsand occur, caused in many cases by pasturing or plowing. A conspicuous instance may be seen just south of Keithsburg, where the railroad passes through a blowout complex, with one large traveling dune.

The Kankakee Area.—This is undoubtedly the largest sand area represented in the state, but at least three fourths of its total extent lies in Indiana. Leverett (*1899:* 328-338) has given a detailed account of its extent and thickness, and from him the following statements are taken. The sand occupies a roughly semicircular area, with the curved edge to the south. Beginning in western Marshall county, Indiana, the sand margin curves to the south and southwest near the Tippecanoe river, passes westward near the towns of Monticello and Kentland into Iroquois county, Illinois, and thence follows the Iroquois river north to the Kankakee river, which forms the northern boundary of the area. This area includes about 3000 square miles (7500 sq. km.). The deepest deposits lie near the Kankakee river, where the sand extends "several feet below the level of the base of the ridges."

As in other areas the sand is not necessarily continuous. Especially near the border of the area it is heaped into irregular ridges and dunes, probably caused by wind, and between them lie areas of sandy loam or muck. As in the Amboy area, the appearance indicates a slow recession of water, with the last of the hydrophytic vegetation still persisting. While the presence of the sand is certainly due to glacial outwash, Leverett does not give more definite conclusions.

At the present time all the upland sand ridges are either forested or under cultivation, while the lowlands of peat, muck, or loam are occupied by swamp or meadow associations. Brief notes on the vegetation, with maps showing the distribution of the sand in Newton and Marshall counties, Indiana, have been published by the Bureau of Soils (Neill and Tharp, *1907*; Bennett and Ely, *1905*). But little attention has been given to this area during the present investigation.

The Winnebago Area.—This series of sand deposits lies chiefly in the northern part of Winnebago county, Illinois, and the southern part of Rock county, Wisconsin. It has been mapped and described by the Soil Survey (Bousteel, *1903b*; Coffey, Ely, and Mann, *1904*). The sand lies between the valleys of Sugar river and Rock river, in

level areas or low ridges with a generally east and west direction, and has a total extent, as estimated by the Bureau of Soils, of 25,088 acres (100 sq. km.).

This sand differs essentially from the other areas described in its upland position. In some places it forms the bluffs of Sugar river, but in the center of its area it occupies the highest ground between the two river valleys and over 100 feet (30 m.) above them. Its position indicates that it is not of fluviatile or lacustrine origin, as stated in the Soil Survey report. Leverett's account of its origin (*1899:* 131-138) is the most satisfactory, connecting the sand with the invasion of the Iowan glaciers. The western border of the Iowan glaciation enters Illinois at the valley of Sugar river, extends south along that river and southwestward along Pecatonica river to the western edge of the county, and thence east to the Rock river. The particular area of sand deposition is thus within the limits of the Iowan glaciers, and the sand itself is regarded by Leverett as the drift of the Iowan invasion.

There is no present evidence of the recent existence of extensive prairies in the Winnebago area. Aside from a few deep depressions with a hydrophytic vegetation, the whole area is either forested or under cultivation.

Climate

The general climatic conditions of the northern and central parts of Illinois are shown in the following diagrams, taken from Henry (*1906*). Dubuque, Iowa, is located on the Mississippi river just north of the Hanover sand area. Beloit, Wisconsin, is situated on the Wisconsin-Illinois state line at the eastern edge of the Winnebago area. Keokuk, Iowa, is on the Mississippi river, near the southern end of the Oquawka area. Springfield, Illinois, is in the central part of the state, east and southeast of the Havana area. Peoria, Illinois, is on the Illinois river, at the northern end of the Havana area. The first four stations, being located at the extreme edges of the general sand areas of the state, will indicate the extremes of climate at the north and south, and the conditions of the intervening region may be approximated by interpolation. Figure 1 shows that the seasonal distribution of heat is of the continental type, with moderately cold winters and hot summers, and with occasional great extremes of heat and cold. It may again be mentioned that the official temperatures, taken under a shelter of regular pattern, do not represent the actual temperature to which plants are exposed. This is particularly true of plants growing in exposed sand, where the surface temperature in

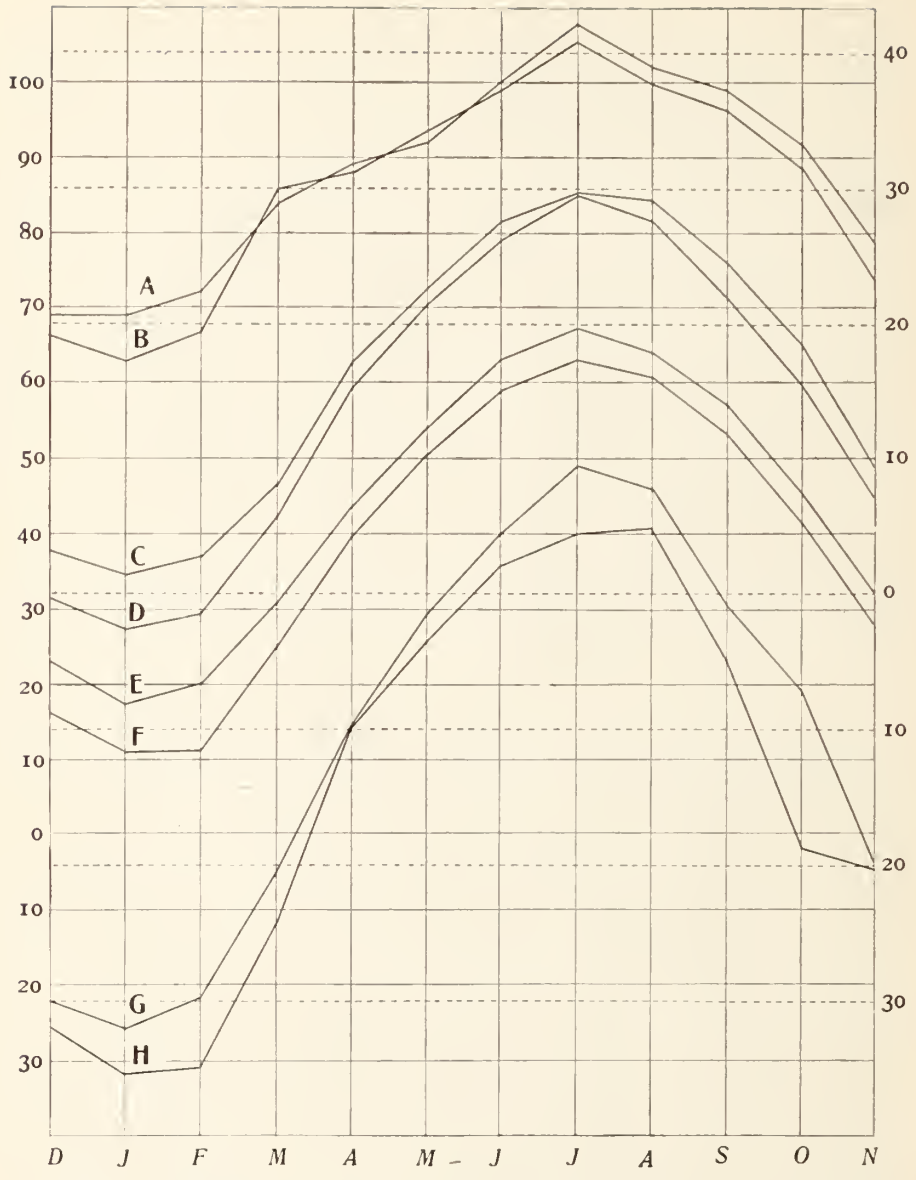

Fig. 1. Temperature curves for Dubuque, Beloit, Keokuk, and Springfield, from December to November, expressed in degrees Fahrenheit (left) and Centigrade (right): *A*, absolute maximum for Keokuk and Springfield, *B*, for Dubuque and Beloit; *C*, mean maximum for Keokuk and Springfield, *D*, for Dubuque and Beloit; *E*, mean minimum for Keokuk and Springfield, *F*, for Dubuque and Beloit; *G*, absolute minimum for Keokuk and Springfield, *H*, for Dubuque and Beloit.

summer may exceed 130° F. (55° C.). According to Mosier (*1903*) the average date of the last frost in spring is April 29 in northern Illinois and April 21 in the central portion, while the first frosts in autumn occur on October 6 and 10, respectively. The average length of the growing season is accordingly from 160 to 172 days, depending on the latitude.

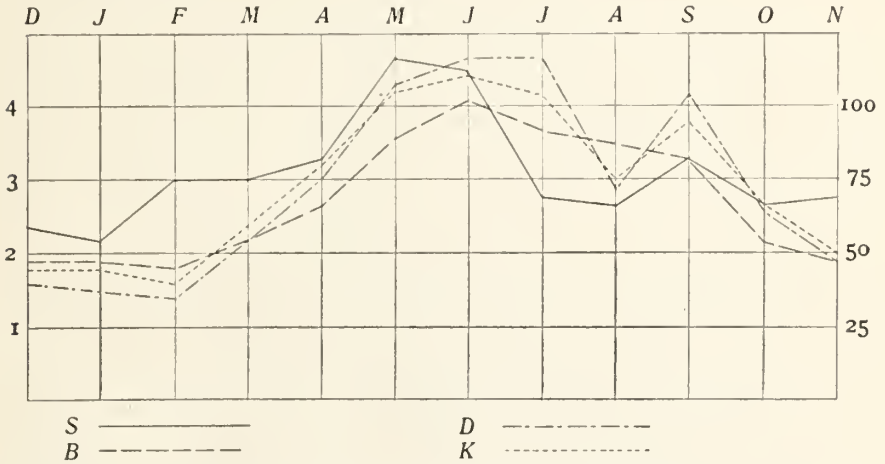

Fig. 2. Rainfall curves for Dubuque, Beloit, Keokuk, and Springfield, from December to November, expressed in inches (left) and millimeters (right).

The rainfall, as shown in Figure 2, is unequally distributed, the greater portion falling during the growing season. The resulting dry winters are probably somewhat favorable to the perpetuation of the prairie formations (Schimper, *1903*). The number of days with 0.01 inch of rainfall or more varies from 75 per year at Beloit to 117 at Dubuque, and of these from 35 to 52 occur during the growing season.

Comparing the preceding statements with the curve of total sunshine (Figure 3), it becomes evident that the comparatively rainy summer months have the greatest proportion of sunshine. This implies heavy rains separated by days of hot dry weather, and leading to a generally xerophytic season in late summer. This climatic feature has already been commented upon (Schimper, *1903*) as in a measure conducive to a prairie type of vegetation.

Further climatological data might be included, but it is believed that these will give a sufficiently complete idea of the general climate of the region. The details of plant distribution are in nowise affected by the broad features of climate.

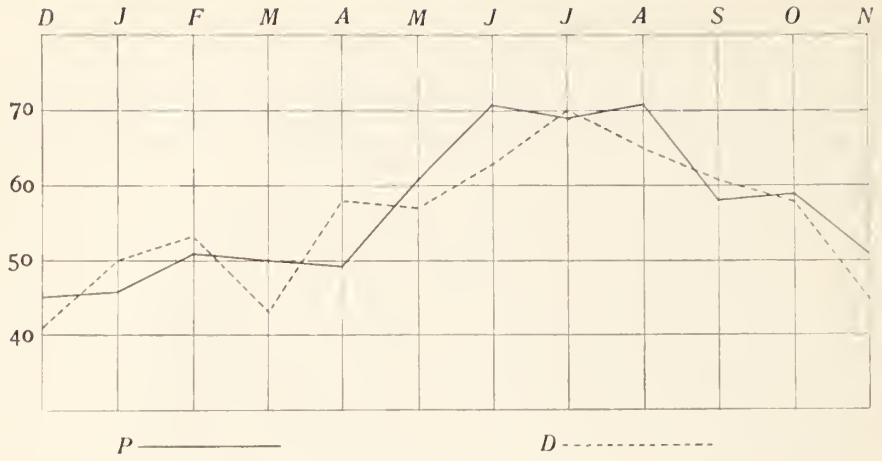

Fig. 3. Sunshine curves for Dubuque and Peoria, from December to November, expressed in per cent. of total possible sunshine.

The Ecological Environment

In each area the sand has essentially the same structure. It is fine grained, yellowish brown in color, and virtually free from organic matter except in the upper layers. In those portions occupied by prairie, and in a part of the forests, the surface is exposed and considerable loose sand is shifted by every wind.

The ecological nature of sand as an environment for plants has been so frequently described that further discussion here is unnecessary, especially since it is probable that no important additions can be made to our knowledge of the subject without careful field experimentation. Some of the best treatments of the matter in English may be found in the works by Cowles (*1899*), Warming (*1909*), Olsson-Seffer (*1909*), and Schimper (*1903*), and in them fuller reference is made to the literature. Briefly summarized, it may be stated that in sand deposits (1) the temperature shows a great variation from day to night and from surface to subsoil; (2) in open associations the insolation is increased by reflection; (3) the water capacity is low and the available supply is small in amount, but constant, because of atmospheric condensations; (4) the amount of soluble inorganic salts and of organic matter is small; (5) in open associations the surface sand is constantly shifting, resulting always in an unstable environment and sometimes in large excavations or accumulations.

Of these conditions, the last exerts the most apparent and the most important influence on the associational distribution of the vegetation.

The other four are probably responsible chiefly for the *selection* of a sand flora from those species which are located within invading distance of the area in question. They certainly can not account for the sharp differentiation of the vegetation into definite associations. In this the plants themselves are most concerned, through their modification and control of the physical features of the environment. If their control is lost, a successional series begins. In the field study, it was usually possible to recognize in the dynamic trend of the vegetation the underlying cause. The descriptions which follow take up the subject from this aspect, discussing in more detail the effect of the dynamic environment, especially the wind, and its partial or complete control by the vegetation.

General Discussion

In the field study upon which this work is based the observational method has been used almost exclusively. No apology or justification for this method is necessary, for direct observation has led in the past and will lead in the future to some of the most important results of plant ecology, and must always be the method by which the first ecological work in any region is done. The value of an exact knowledge of some of the physical features of the environment is evident, but their evaluation in an area of considerable size is a task not to be undertaken by one man or completed in a single season. Undue emphasis on the environment may lead to the partial neglect of the most important feature of a region, the vegetation. The plant itself is in many cases the controlling agent in the environment; the differentiation of definite associations is mainly due to the interrelation of the component plants; and the physical environment is as often the result as the cause of the vegetation. The relative importance of the plant covering and the physical environment is happily expressed by Spalding (*1909:* 477, 479): "But little reflection is needed to arrive at the conclusion that the classical question regarding the relative importance of physical constitution and chemical composition of the substratum to plant growth * * * does not, and can not reach the heart of the problem. * * * This being the case, it would seem that in the future, investigations of the habitat relations, of the desert species especially, must be directed mainly to the plant itself. * * * The establishment of a plant in the place which it occupies is conditioned quite as much by the influence of other plants as by that of the physical environment."

In the prairies of the sand deposits the two chief dynamic features

of the environment are wind, which tends to move the sand, and vegetation, which tends to stabilize it. These two opposing forces are primarily responsible for the present location of every association. In the forested portion of the sand the water factor is apparently the most important, but it depends chiefly upon the influence of the vegetation rather than upon any truly physical condition. In a broader way, the presence of a particular flora in the sand is due partly to the selection from the surrounding associations of various species with certain physiological requirements, and partly to climatic changes in the past. The latter can only be conjectured; the former are not known for any plants in this state and for very few in any place. According to these views, physical factors are relatively little concerned in the development of vegetational structures in this region, while the demands of the plant and the effects of its growth are of chief importance.

The delimitation of the various associations concerned is also a matter which must depend, for the present at least, upon direct observation. Jaccard (*1902*) has given a method for comparing different associations and stating numerically the degree of difference between them. This has been used frequently and has given some comparisons which are interesting rather than important. It can not, however, be used successfully in the field. The chief difficulty in separating associations lies in the idea of the association itself, which has never been expressed with sufficient clearness.* By some this idea has never been received with favor. It is true that the distinctness of the associations is lost and their character greatly modified by the effects of civilization, but experience in natural conditions justifies the statement that associations are definite organized units and that all vegetation is composed of them, either mature and fully differentiated or in process of organization (cf. Harper, *1906:* 33, 34). It is as difficult to formulate a satisfactory definition of an association as of a species, and as unnecessary. For the present it may be considered that it is a homogeneous area of vegetation in which the interrelations of the component individual plants permit them to endure the physical environment.

In this work the recognition of associations has been based upon the idea of uniformity, and those areas, whether large or small,

* The concepts of the association as expressed by authors are very variable and frequently conflicting. Some demand that each association shall occupy a definite habitat (Clements, *1905:* 292), others allow a wide range in environment (Cowles, *1901:* 79); some consider that the change of a single species affects the nature of the association (Harshberger, *1900:* 652), while others permit a large variation in the flora (Warming, *1909:* 145, 146).

which are homogeneous (Clements, *1904:* 11) throughout their extent have been considered members of the same association. This uniformity is shown by the environment, by the behavior of the vegetation, and, above all, by the plants themselves.

In a region of limited size, over which the climate is essentially the same, the physical environment of an association is usually nearly constant, although instances are not lacking of an association living in the same area under widely different conditions (Cowles, *1901:* 79). On the other hand, it is not necessary that every area with the same environment should be occupied by one association. It is regularly the case in the sand region, and usually also elsewhere, that if the areas of the associations are conditioned by the environment, a considerable and observable change is necessary to influence the vegetation (Clements, *1905:* 292). But in no case should the recognition and delimitation of associations be based upon the environment alone, which leads to a classification of habitat rather than vegetation (Gradmann, *1909*) and may lead to the uniting of radically different types of vegetation.* The behavior of the vegetation with respect to adjacent areas is shown by successions which take place between them. If two areas with essentially the same environment show no successional relations it is probable that they represent different consocies of the same association.

But the first test of a plant association must be the vegetation itself. No two areas of vegetation are exactly similar, either in species, the relative number of individuals of each, or their spatial arrangement, and the smaller the areas to be compared the greater proportionately are the differences between them. Also, with continued and more detailed observation the importance of these minor variations is magnified, and tends to lead to the recognition of an unwieldy number of minor groups unworthy of the rank of association. This introduces the question of how great a variation may occur in the structure of the vegetation without the identity of the association being changed. Field work shows that the dominant and the secondary species may both vary independently. In the same association the dominant species, if more than one, will have the same vegetative form, as bunch-grasses, or trees, and will be of nearly the same size. Excessive development of one of them to the partial or complete exclusion of the others makes no change in the general ap-

*The classification of associations by Clements (*1905:* 302, 303) is largely of this nature, and in some cases leads to the wide separation of closely related associations or even to the placing of a particular area in two different groups. Thus a hydrophytic sand-bar (*cheradium*) may be converted into a new xerophytic "formation" (*syrtidium*) merely by the fall of the water in the river.

pearance of the vegetation and does not affect the growth of the secondary forms. There are frequently no successional relations between these local areas, or consocies. Areas characterized by dominant species of widely different appearance can not be regarded as belonging to the same association unless it can be shown that the areas represent transitory stages of development, as described below for the stabilization of blowouts. If the dominant species have the same general form, but do not tend to mix, except in the tension zone between them, and are accompanied by different groups of secondary species, the occurrence of different associations is suggested, as in the black oak and bur oak forests.

The secondary species occupy a comparatively small area in the associations and their number usually depends in some way upon the habits of the dominant species. This is well illustrated by the bunch-grass association, in which the secondary species are absolutely dependent upon the dominant bunch-grasses. More species are concerned and their distribution is frequently irregular. These irregularities, however, are seldom coincident with any variation in the dominant plants, but are caused chiefly by competition for space regulated by seed dispersal and seasonal climatic fluctuations. A considerable variation in their quantitative distribution may be expected, unless they belong to the derived element of the association (see below), in which case they may indicate the beginning or the end of a succession or some local change in the environment which is nevertheless not sufficient to induce a change in the dominant species.

Two areas of vegetation dominated by different species are accordingly probably consocies of the same association if (1) there is no obvious difference in their environments; (2) if there is no evidence of succession between them; (3) if the secondary species are the same for each; (4) if the dominant species are of the same vegetative form or (5) tend to mingle in other areas with the same environment and secondary species.

A slight deviation from these criteria may be neglected if there is a preponderance of agreement with them, while a radical deviation would indicate that the areas represent distinct associations. In most cases (in the sand areas, at least) their application in the study of the vegetation leads to definite and unquestionable results.

Whether small or large, associations usually contain some species which are more characteristic of other areas. This *derived element* can be recognized only by comparison with neighboring associations, where the species in question are more numerous, more general in distribution, or more luxuriant in growth. They are least abundant

near the center of the association, and tend to increase progressively toward its boundaries. The best idea of the structure of an association is accordingly gained at its center. The presence of a derived element is well illustrated in the black oak association, in which every spot of unshaded exposed sand is occupied by interstitial annuals of the bunch-grass association, while near the margin of the forest numerous prairie perennials and grasses also occur. Many species, naturally, are almost equally typical of two or more associations.

The boundary of an association is frequently sharp and well defined, especially if the dominant species of the adjoining areas are of different vegetation forms, as between prairie and forest, or if the associations are correlated with considerable and relatively constant differences in the environment, as between the windward slope and basin in the blowout formation. In other cases the boundary is broad and more or less indefinite. This is particularly true if the dominant species are of the same vegetation form or if the environmental difference is fluctuating, as, for example, between the bunch-grass and the *Panicum pseudopubescens* associations. The vegetation of these transition zones is a mixture of usually indefinite and frequently highly variable character. The species in them should be referred as far as possible to their respective associations, and not allowed to modify the ideas of structure gained from an examination of more typical localities.

Besides these transitions in space, there are also transitions in time. An early stage in the development of an association may resemble but little its mature condition. Certain members of the association with excessive seed production, with more mobile seeds, or better adapted to the somewhat aberrant environment, appear first and for a time dominate the area. Thus, in the stabilization of a blowout, the redevelopment of the bunch-grass association begins with a growth of *Lespedeza capitata* and *Oenothera rhombipetala* in large quantities. This condition lasts but a short time before they are replaced by the usual bunch-grasses. Such an area is at first suggestive of a distinct association, but examination shows that it has no species, aside from relics of the preceding vegetation, not found also in the bunch-grass, and that the environmental conditions are very similar to those of the spaces between the bunches of grass, where these interstitials (p. 54) grow. A knowledge of the habitat preferences and habits of the component species and of the general dynamics of the area is necessary to decide upon the proper classification of these transitional stages.

In estimating the uniformity of the vegetation, direct observation

is in many cases satisfactory, especially if the associations are small in area or the component plants low in stature so that a comprehensive view of them may be taken. In other cases, simple lists of species, taken in each area of the association, may be compared, and their similarity is a good index. For more accurate work, the quadrat method proposed by Clements (*1905:* 161-170) may be employed. It gives excellent results but demands much time and labor. In areas of closed vegetation it seems to have its chief value in expressing, rather than determining, the structure of the association. A modification of the quadrat method has been tried with success in this work. It consists in listing, in the approximate order of the space occupied by each (not the number of individuals), the species on an imaginary quadrat of about four square meters situated directly in front of the observer. Stepping forward two paces brings another quadrat to view, and a series of ten or twenty, extending in a continuous strip or scattered throughout the association, may be listed in a short time. The size of the quadrat used is chosen to suit the character of the vegetation; two meters square seems adequate in the study of prairie associations. In a forest a quadrat of that size could be used only for the herbaceous vegetation, and one ten meters square would be necessary to show the nature of the forest cover. Quadrats of such size are unwieldy, and in practice it has been found that results are more easily obtained by counting every tree within five meters of the observer as he walks through the forest. A new list may be made for each hundred meters or for any area with distinct environment.

In investigating the tension zone between associations the transect method (Clements, *1905:* 176-179) may be used, but is subject to the same limitation as the quadrat method. Good results may be conveniently obtained by walking back and forth repeatedly from one association to the other, listing the species in the order of their appearance.

Carefully conducted studies, as indicated above, show that the dominant species are uniformly distributed over the whole area of the association or consocies, and that the floral discrepancies are caused by a number of comparatively rare species represented usually by a small number of individuals. The weakness of the whole method lies in the fact that, in a mere list, a rare species, possibly a single individual, is given as much weight as a common one. Actual counts of the individuals of each are difficult to make and may give misleading results. If each species could be correlated with the proportion of the area which it occupies, it would be demonstrated that most parts of an association are highly similar in structure, and the

resulting community coefficient of different areas would probably be above 0.900 (in the black oak association virtually 1.000). Unfortunately no practical method for this has been devised.

The more widely the different areas of an association are separated, the greater are the floral discrepancies. The dominant species, however, remain constant, and the change lies almost wholly in the secondary species. Many of these are the results of selective migration from neighboring associations, so that a variation in the general nature of the vegetation of an area affects the specific structure of each association. This phenomenon has been discussed briefly by Warming (*1909:* 145, 146) under the name of geographical variation. It is well illustrated in the sand areas of Illinois by the secondary species in the black oak association. In the Havana area are found some typically southern species, as *Quercus marilandica* and *Galium pilosum*, while in the Winnebago area some species of northern or eastern distribution occur, as *Pyrus americana* and *Lupinus perennis*. In comparing areas of such wide geographic separation emphasis must be placed upon the dominant species, which are the fundamental cause of the general physiognomy of the association.

The areal distribution of an association may be compared to the distribution of a species. Both are irregular in outline, although coextensive with certain combinations of environmental factors. Both consist of scattered members, independent of each other, but related by a common genesis and common demands upon the environment. Both show minor local and broad geographical varieties. The former are illustrated in the association by the consocies; the latter, in the species by the subspecies, which in their typical form occupy outlying arms or peninsulas but toward the center of distribution intergrade with the main body of the species. Taxonomic work has shown that the interpretation and classification of these forms is a matter of great difficulty. Proper treatment of the geographical varieties of an association will be a matter of much greater difficulty, since the necessary comparisons must be based entirely upon written description or photographic record.

Because of this geographical variation and consequent difficulty of comparison, few correlations of associations in different parts of America have been made or attempted. Ecological literature contains numerous descriptions taken from the few representatives of the associations in a limited locality, but as yet no one has given a general description of an association, compiled from observations taken

throughout its range.* In this respect the present status of systematic ecology resembles that of pre-Linnaean taxonomy, a maze of detached facts waiting for a Linnaeus to collate and correlate them into a foundation for future investigation.

The associations recognized in the field have been grouped into formations, characterized partly by uniformity in the physiognomy of the vegetation, and partly by uniformity of environment, to which the physiognomy is in some extent due. Formations correspond somewhat to genera in taxonomy, and like them may be limited or comprehensive in their scope, this depending solely upon individual opinion. As far as possible they have been made to coincide with the popular idea of the different types of vegetation. The four formations are all generally known through the sand regions and given the names used here, with the exception of the forest, which is colloquially known as "timber" or, in some places, as "black-jack." The latter term applies to the particular association rather than to the forest formation in general. The areal extent of a formation is approximately coincident with one of the phytogeographical provinces of North America, and formations with the same distribution are placed in the same province. It is thus seen that the differentiation of both minor and major ecological groups depends principally upon the plants themselves, the associations being distinguished by the specific composition, the formations by the general appearance, and the province by the distribution of the vegetation. This is an extension of the idea already expressed, that the most important feature of the association is not the habitat but the plant. It is believed that the regional classification of associations is really genetic and dynamic, bringing together those which are most closely related by origin and succession.

The Vegetation

The area covered by the state of Illinois occupies a unique position in respect to the vegetation of the continent, marking the region of closest approximation of four great floral and vegetational provinces. (See maps in Schimper, *1903*; Engler, *1902*; Transeau, *1903*, *1905*; Merriam, *1898*; Sargent, *1884*.)

The Austroriparian Province (Merriam, *1898:* 45) enters the state at the extreme southern end, and well-developed examples of its dominant hydrophytic vegetation, the cypress swamp (*Taxodium distichum*), extend northward into the lower valley of the Wabash

*The nearest approach to this has been made by Transeau (*1903: 1905-6*) in his studies of bog floras.

river. Scattered species of Austroriparian affinity extend north in ever decreasing numbers, for some 300 miles (500 km.). One of the most conspicuous plants of this nature is *Carya illinoensis,* the pecan, which follows the alluvial bottom-land of the Mississippi river as far as southeastern Minnesota. Few species of this group occur on the sand deposits of northern and central Illinois, although a number occupy the sand-bars of the lower Mississippi.

The southern boundary of the great Northeastern Conifer Province of the north and northeast passes southeastward across Wisconsin and Michigan, and numerous species persist south of this line. Definite but isolated associations of *Pinus Strobus* and of *Larix laricina,* each with its usual attendant species, are found in various places in northern Illinois, and many scattered species of northern range, such as *Populus tremuloides* and *Betula alba,* var. *papyrifera,* live in associations of other provinces. Some of them are concerned in the vegetation of the sand deposits.

Between the Austroriparian Province on the south and the Northeastern Conifer Province on the north there are extensive plains, reaching from the base of the Appalachian mountain system on the east to Nebraska on the west. This area is known as the Deciduous Forest Province, and is occupied, as its name indicates, by deciduous forests, with *Quercus, Acer, Fraxinus, Tilia, Fagus, Nyssa, Liriodendron, Aesculus,* and *Carya* as some of the leading genera. In the eastern part of the province the forest is almost continuous, broken only by minor associations of an edaphic nature. At the west, from Indiana and Illinois to Nebraska, it becomes discontinuous, and a portion of the area, becoming proportionately larger westward, is occupied by the prairies.

The Prairie Province, last on the list, extends in a long strip north and south through the Great Plains at the eastern base of the Rocky Mountains from Texas to Saskatchewan, and an eastward extension passes across Iowa and Illinois into Indiana, sharing the area with the deciduous forests (Pound and Clements, *1898*). Throughout its whole area the dominant vegetation is prairie.

Each of these four provinces is composed of many plant associations, which occupy usually definite habitats, and which are related to each other by certain successional trends. In each there are associations occupying limited areas of extreme environment, and these tend to converge, through the effect of various physiographic and biotic agencies, toward the dominant or climax vegetation of the region. In each of the provinces the successional events in the establishment of the dominant vegetation are relatively simple. There

is in every case at least a hydrophytic and a xerophytic extreme, forming two general converging lines of succession. In our present knowledge of the subject, it is impossible to state whether there is one definite climax association in each province; it seems probable that there are several such associations, each characteristic of a limited portion. It is certain that in each province there is a dominant *formation,* or type of vegetation, deciduous forest, coniferous forest, or prairie, as the case may be. Present evidence seems to indicate that the nature of the dominant type is determined by a long chain of historical factors (Adams, *1902*, *1905*) and its present areal distribution by the broader existing climatic factors, notably heat and rainfall (Transeau, *1905*).

The boundaries of the four provinces have been subject to great changes in the past, both during and following the glacial period, as the ice swept to the south, overthrowing the previous conditions of climate, and then retreated to the north, uncovering unoccupied ground and throwing it open to plant invasion. The ensuing movements of vegetation were among the greatest in the history of the continent, and have been of the greatest moment in determining the present distribution of the biota.

These movements have by no means ceased. They are merely less obvious when measured in terms of years and centuries rather than in geological periods. Even now a biotic migration is in progress, which is probably the direct continuation of early postglacial movements, and is doubtless as rapid and as far-reaching in its effects as any of the past.

In the present migration the vegetation of the Deciduous Forest Province is the chief factor. It is now pushing out its boundaries to the north and west and enlarging its area at the expense of the Northeastern Conifer Province on one side and the Prairie Province on the other. Some detailed features of the northern extension have been given by Whitford (*1901*), Transeau (*1905-06*), and others, and summarized by Adams (*1905*). The westward migration has been mentioned by many, but scarcely described in detail.

The actual steps in the migration of the vegetation are due to a series of successions, by which associations of the prairie or of the coniferous forest are replaced by others, with similar environmental demands, from the deciduous forest. Some of the northern and western associations are succeeded with comparative ease; others resist succession for long periods of time. Because of this the forest extends north and west, not in continuous masses but in long tongues and detached bodies, while relics of the former vegetation lag be-

hind as isolated areas in the midst of the forest. Relics of the northern coniferous forest persist in Illinois as tamarack swamps and groves of white pine, and both are frequently termed "boreal islands." In a similar way the detached areas of prairie in Illinois may be regarded as western relics, although they are often miles in extent. The oldest relics, that is, those toward the east or south, are regularly smaller in extent and more mixed with forest species (Bonser, *1903*). In the migration of the deciduous forest associations, the greatest advance has always been made in those habitats which most nearly resemble those occupied by the climax formation, and which are therefore most nearly suited to the invading vegetation. On the other hand the relic associations have been left behind in those habitats, not necessarily best adapted to the relic vegetation, which are least suited to the invaders. For this reason the boreal associations in Illinois are limited to sandstone hills and to undrained swamps, while the prairies persist chiefly in the upland soils between the stream courses.

The successions by which the general migration is consummated are of a type different from that found within the formation and leading merely to the dominance of the climax vegetation, since they involve associations of two and sometimes of three provinces. While several descriptions of this type have been published, general conclusions have not usually been drawn. At the present time it can only be stated that the succession seems to take place between equivalent members of the different provincial successional series. Thus, as shown in the following pages, the xerophytic extreme of the prairie, the bunch-grass association, tends to give way to the corresponding extreme of the forest, the black oak association. In a similar way the black oak association may succeed the xerophytic extreme of the Northeastern Conifer Province, the jack-pine association. We find similar relations between the hydrophytic extremes, and in Illinois the succession of the northeastern tamarack association by the deciduous bottom-land forest may be observed.

Northern Illinois, therefore, has been and is the scene of important events in the biogeographical history of the continent. The following description of vegetation is designed to be not merely a discussion of static conditions, but rather a portrayal of one phase of this great vegetational movement and of the consequent struggle for supremacy which is still being waged.

In the vegetation four distinct formations, or types of vegetation, have been recognized. Each of these consists of several associations, characterized by a distinct group of plants, by a distinct habitat, or by

both. The subjoined tabular view will express the classification used, while the arrangement of the associations in the descriptive matter follows as nearly as possible their successional relations.

Classification of the Plant Associations

A. The vegetation is dominated by grasses, occupying a relatively stable habitat with low water-content. The secondary species occupy the interstices between the stools of grass. The Prairie Formation of the Prairie Province.

a. The movement of sand is slow; several species of bunch-grass are present and many secondary perennial species.
The Bunch-grass Association.

b. Sand movement is more rapid; the area is dominated by *Panicum pseudopubescens* and the secondary species are chiefly annuals.
The *Panicum pseudopubescens* Association.

B. The vegetation is very sparse and open, occupying usually a very unstable habitat due to rapidly shifting sand; there is little distinction between dominant and secondary species. The Blowout Formation of the Prairie Province.

a. The sand movement is chiefly due to removal by gravity; the vegetation consists of relic grasses and perennials.
The Windward Slope Association.

b. The sand movement is due chiefly to removal by wind; the extremely sparse vegetation consists of deep-rooted perennials.
The Basin Association.

c. The sand movement consists chiefly of a mere redistribution or of gradual deposition; the vegetation is composed chiefly of annuals.
The Blowsand Association.

d. The sand movement consists chiefly of a mere redistribution; the vegetation is dominated by the sand-binding perennial, *Hudsonia tomentosa*.
The *Hudsonia* Association.

e. The sand movement consists chiefly of deposition; the vegetation is composed of sand-binding perennials with accessory annuals.
The Deposit Association.

f. The vegetation occupies a fossil soil, uncovered by continued sand movement; the dominant species is *Stenophyllus capillaris*.
The *Stenophyllus* Association.

C. The vegetation is dense, closed or nearly so, with grasses only as secondary species; the sand is stable, with usually relatively high water-content; the formation is developed in deep depressions.
The Swamp Formation of the Deciduous Forest Province.

a. The vegetation is semixerophytic, characterized by slender perennials.
The *Solidago* Association.

b. The vegetation is truly mesophytic.

1. The vegetation is dominated by willows. The *Salix* Association.
2. The vegetation is dominated by mat-forming mosses.
The *Polytrichum* Association.

c. The vegetation is hydrophytic.....The Swamp Association.

D. The vegetation is dense and closed, dominated by trees or avevectent shrubs, or by herbs in the immediate vicinity of shrubs; the sand is stable, with usually low water-content.

The Forest Formation of the Deciduous Forest Province.

a. The vegetation is dominated by herbs.

The *Smilacina* Association.
The *Physalis* Association

b. The vegetation is dominated by shrubs, with numerous lianes, the secondary species are of a mesophytic type.

1. On the crests of dunes or other areas of deposition.

The Dune Thicket Association.

2. In blowouts.....The Blowout Thicket Association.

c. The vegetation is dominated by trees.

1. The secondary species are generally xerophytic; avevectent shrubs or lianes are few or absent; the leaf-mold is thin or absent.

The Black Oak Association.

2. The secondary species are generally mesophytic; avevectent shrubs and lianes are abundant; a superficial layer of humus is developed.

a. The dominant species are bur oak and white oak.

The Bur Oak Association.

b. The dominant vegetation is composed largely of black oak, but with numerous other arboreseent species.

The Mixed Forest Association.

The Prairie Formation

The bunch-grass association

The bunch-grass association formerly occupied probably more than nine tenths of the unforested portion of the sand areas. It extended over hill and dale, interrupted only by the blowouts and their related associations, and was by far the most important association of the unforested area. Monotonously uniform floristically, its ecological structure showed an obvious differentiation into several consocies, each characterized by the preponderance of one or a few species of grass, and often sharply distinct from its surroundings. These are considered to be consocies instead of associations because they can not be referred to any apparent difference in the environment, and because they exhibit no successional relations to each other.

The best development of the bunch-grass association was, and is, in the Hanover sand area. By far the larger portion of the area was originally unforested. Large fields are still in a virgin condition, and hundreds of acres have been but little pastured. The area includes most of the consocies described and offers without doubt the best conditions for ecological study. The Winnebago area includes, so far as observed, but one small area of bunch-grass, not more than an acre in extent, entirely surrounded by forest. It is evidently a

relic of a former wider extension of the association. In the Amboy area most of the country is either forested or pastured, and the only observed examples of bunch-grass were scattered fragments along the roadsides. The Dixon area formerly contained much bunch-grass, but it is also now largely under cultivation. The Oquawka area is more extensively forested, but some of the bunch-grass still remains in the original condition. The *Leptoloma cognatum* consocies is especially well represented there. The bunch-grass association formerly occupied thousands of acres in the Havana area, but most of it is now under cultivation.

In the three chief sand areas, at Hanover, Oquawka, and Havana, the sand deposits lie, as has already been noted, on the east side of a river, extending from the water's edge to the bluff. The bunch-grass association is always separated from the river by a narrow or wide marginal forest, but may extend inland to the very base of the bluffs, as at Hanover. It may then be divided into smaller areas by transverse belts of forest, as at Havana. To these smaller tracts local names are sometimes given, as Benton Prairie at Oquawka. The tracts thus delimited are not uniform, but each may be occupied by two or more consocies. The different prairies of a sand area are, however, occupied in general by the same consocies and have the same flora. But two noteworthy species seem to form an exception to this rule, *Brewcria Pickeringii* in Benton Prairie at Oquawka, and *Lesquerella argentea* in the Devil's Neck region of the Havana area.

The bunch-grasses which give the association its name produce at the base or along the lower portion of the culm a number of leaves, which are aggregated into loose or crowded bunches, depending upon their size and number. Rising from their center are the flowering culms, and beneath the living leaves are also the dried dead leaves and culms of the previous season. The height of the bunches, exclusive of the culms, is therefore, in most cases, approximately equal to the length of the basal and lower leaves. In simple bunches all the leaves and culms radiate from one center, and a bunch consists of one plant, or rather of one stool. The diameter of the bunch is then not more than twice the length of the basal leaves. Such simple bunches are exhibited by *Panicum perlongum* and *Stipa spartea*. With some other species, as *Panicum pseudopubescens*, the culms are also spreading or horizontal, and the diameter of the bunch is about equal to twice the length of the culms. In other cases the individual plants are closely associated, so that the dense bunches may reach any diameter, and are usually very irregular in shape. This

habit is well illustrated by *Leptoloma cognatum*. The bunches of each species are distinct in size, structure, and general appearance, and when in a sterile condition can frequently be recognized by their habit alone. Notes on the individual character of the bunches will follow.

The living and dead leaves of the bunches cover the ground in most cases so closely that other plants can not grow among them. The two bunch-forming sedges, *Carex Muhlenbergii* and *Cyperus Schweinitzii*, alone produce bunches so loose that various annuals usually grow within them. *Stipa spartea* also produces loose bunches through which *Ambrosia psilostachya* or *Teucrium occidentale* may grow. A number of small annuals may be found between the radiating culms of *Panicum pseudopubescens* at some distance from the center, while the dense compact bunches of *Koeleria cristata* and *Leptoloma cognatum* are entirely free from other plants.

Besides restricting the growth of other species, and thus retaining the dominance in the association, they act efficiently in preventing the blowing of the sand. The greater proportion of the surface is usually entirely covered, and the small intervening spaces are so narrow that the sand is not easily lifted by the wind above the bunches. The tendency to blow, if present, is usually shown by the slight elevation of the grasses above the concave or trough-shaped interspaces. Nevertheless, blowing may sometimes take place to such an extent that the whole association is destroyed, and succeeded by another in which *Panicum pseudopubescens* is the dominant grass, as will be described later. It seems probable that in most of these cases the density of the plant covering has been reduced by pasturing or other recent causes, or, conversely, that under strictly natural conditions the bunch-grasses permanently prevent blowing.

In some places the surface is entirely covered, either with bunch-grasses alone or with mat-plants in addition, and there is every gradation down to cases where but little more than half the actual surface is occupied. It may be arbitrarily assumed that the bunch-grass association can not exist with more than half the sand exposed, and it is certain that it may disappear with even more of the surface occupied. The proportion of the ground covered by the grasses varies with the species, the habitat, and the stability of the sand. Of the grasses which tend to cover a relatively small part of the surface *Koeleria cristata* and *Andropogon scoparius* are good examples, while the bunches of *Leptoloma cognatum* show especially a tendency to become confluent and to cover large unbroken areas. The consocies which contain the largest number of species of bunch-formers are also apt to occupy the space most completely.

The general appearance of the association, including especially the color-tone and number of secondary plants, depends almost entirely upon the specific peculiarities of the bunch-grasses represented and upon the density of the covering. Most bunches are so distinct in size, density, or other features that they are easily recognized, even when sterile. In doubtful cases minor morphological characters may be used, such as pubescence, the structure of the ligule, and other similar vegetative features. Some of the most important bunch-forming species are the following.

1. *Koeleria cristata.*—Bunches regular, compact, about one foot (3 dm.) in maximum diameter and eight inches (2 dm.) high, with a considerable accumulation of dead leaves beneath them, forming an elevated central tuft and radiating on the sand; leaves six to ten inches (15-25 cm.) long, mostly straight and erect, glaucous-green or canescent with fine pubescence.

The regular close bunches of *Koeleria* have an appearance of trimness and neatness in which they excel any other species. The gray-green color and the shining spikelike panicles make the grass very conspicuous, especially during the aestival aspect when it is in bloom, or at any season when the dew is still on it in the early morning. The bunches are rarely confluent and tend to leave a considerable uncovered area between, especially when not associated with other species.

2. *Leptoloma cognatum.*—Bunches 8-12 inches (20-30 cm.) wide and about eight inches (20 cm.) high, very compact, close and dense, flat-topped, frequently confluent in large irregular patches; leaves short, all erect or radiating, and freely mixed with the dead leaves of the preceding season, giving the whole bunch a yellow-gray appearance. The short leaves are more irregularly arranged than those of *Koeleria cristata,* and the dead leaves and culms remain for a long time mixed with the living. In the serotinal season the large, but very lax, red-flowered panicles appear and impart a distinct reddish hue to the consocies in which the plant grows.

3. *Stipa spartea.*—Bunches loose, few-leaved, but regular in size, 1-1.5 feet in diameter and about the same height, with a slight accumulation of dead leaves and culms on the sand beneath. The flowering culms rise to a height of three feet (1 m.). Of all the bunch-forming species of grass in the association this species forms the loosest and most indefinite bunches.

4. *Panicum pseudopubescens* (Pl. III, Fig. 2).—Bunches irregularly circular in outline, depressed, 1-1.5 feet (3-5 dm.) in diameter, four to six inches (1-1.5 dm.) high; culms and leaves radiating from

the center, straight, barely exceeding the dead culms with their split and curled leaves. The culms and especially the spikelets are red in color and give a reddish tone to the whole bunch.

This species forms one of the most distinctive bunches of the association, due to the depressed or prostrate radiating culms with their erect or almost appressed leaves, and to the persistence on the dead culms of the recurved leaves of the previous season. The culms extend beyond the leaves, and bear small, but conspicuous, panicles of red spikelets. This species is more characteristic of the association to which it gives its name, but is also frequent in the typical bunch-grass, where its peculiar habit makes it conspicuous.

5. *Bouteloua hirsuta.*—Bunches low, irregular, two to four inches (5-10 cm.) high, usually confluent in matlike masses 5-12 inches (1-3 dm.) in diameter; leaves short, irregular in position, forming a loose tuft, conspicuously gray-pubescent, and giving a gray color to the whole bunch. The slender culms, 4-12 inches (1-3 dm.) high, appear during the late aestival season. The small bunches are entirely too low to compete with the other grasses for space or to constitute a conspicuous element in the association. They are usually restricted to the intervening spaces, where they have the general habit of mats rather than of bunches. They associate frequently with *Selaginella rupestris.*

6. *Bouteloua curtipendula.*—Bunches loose, 6-12 inches (1-3 dm.) in diameter, eight to ten inches (2-3 dm.) high; leaves mostly all erect, six to eight inches (15-20 cm.) long.

7. *Cyperus Schweinitzii.*—Bunches very open and loose, basal leaves few in number, ascending; culms several, erect or ascending. The plant frequently has the habit of an interstitial rather than of a bunch-grass.

8. *Andropogon scoparius.*—Bunches one to three feet (3-8 dm.) wide, circular, 1-1.5 feet (3-4 dm.) high, compact, and regular; leaves very long and narrow, erect or ascending, the dead leaves persisting as a dense mass at the base, or recurved around the margin of the bunch; culms about two feet (6 dm.) high, the dead culms persisting through the following summer.

The bunches are notable for their large size and the dense mass of dead leaves mingled with the living ones. As the bunches grow older the center dies, and rings are formed which reach a maximum diameter of over a yard (1 m.). In such rings the zone of living grass is three to eight inches (1-2 dm.) wide, and the central portion is elevated four to six inches (10-15 cm.) above the general level. It is composed of a dense mass of old roots and culms mingled with

debris of all kinds, and is almost always devoid of any plant growth.

9. *Andropogon furcatus.*—The bunches of this grass, commonly known as bluejoint, resemble those of the smaller *A. scoparius* in general habit, but are taller, 1.5-2.5 feet (4-8 dm.), and frequently larger in diameter, three to four feet (8-12 dm.). The leaves are larger, less densely aggregated, and without the tangle of dead leaves among them. The flowering culms are three to five feet (10-15 dm.) tall or even more, and seldom persist until the following summer. Like *A. scoparius,* the bluejoint may also form rings by the death of the center of the old bunches. These are five to seven feet (15-20 dm.) in diameter and without a conspicuous elevated center.

Sorghastrum nutans and *Panicum virgatum* (Pl. IV, Fig. 2) form large bunches much resembling those of bluejoint. *Calamovilfa longifolia* grows in patches with the individual culms one to six inches (3-15 cm.) apart, forming dense clusters which resemble true bunches. *Eragrostis trichodes* produces bunches closely resembling those of *Andropogon scoparius* in general character, but without the mass of dead leaves. The bunches of *Panicum perlongum* are very regular, hemispherical in shape, and composed of a dense mass of straight radiating leaves. In general appearance they resemble the bunches of *Koeleria cristata. Paspalum setaceum* and *Eragrostis pectinacea* send up several culms from a common center, on which the leaves are most closely approximated near the base, thus forming a loose irregular bunch. The loose open bunches of *Carex Muhlenbergii* are especially characterized by their leafless, obliquely ascending stems.

Since the bunch-grasses virtually exclude other growth beneath them, the secondary species are found upon the small areas of bare sand between the bunches. They may be conveniently divided into four ecological groups based upon their habits and structure. As in most ecological classifications, these groups are not entirely distinct, and some species are of doubtful position. To them may be given the names perennials, mats, interstitials, and parasites.

The members of the first group, the perennials, are generally very deep-rooted, and frequently grow in tufts or bunches resembling those of the bunch-grasses. The deep roots are a response to the conditions of water supply, and the bushy habit is possibly correlated with the generally xerophytic environment and exposure to the wind. Resembling the bunch-grasses in habit, they are able to compete with them for space, and may be found in the center of a patch of grass, where they have persisted since the grass surrounded them. Their

competition with the bunch-grasses is defensive rather than offensive; they can resist the encroachment of a grass, but are not able to displace it. Some typical plants of this habit are *Aster linariifolius, Lithospermum Gmelini, Aster sericeus, Tephrosia virginiana* (Pl. IX, Fig. 1), and *Chrysopsis villosa.* Others have more slender stems, several of which arise from a common base and spread divergently, somewhat resembling in habit the looser bunches of *Carex Muhlenbergii* or *Cyperus Schweinitzii.* Good examples of this type are furnished by *Callirhoe triangulata, Petalostemum purpureum,* and *Petalostemum candidum.* Still others have erect stems which tend to grow in clusters, as *Corcopsis palmata, Solidago missouriensis, Solidago nemoralis, and Helianthemum majus.* A fourth type is furnished by *Physalis virginiana, Baptisia bracteata,* and *Tradescantia reflexa,* with solitary stems which branch freely or bear widely spreading leaves toward the top. A fifth type is illustrated by *Euphorbia corollata* or the species of *Liatris,* whose slender erect stems grow singly and occupy very little ground space. This type approaches most nearly the third group of interstitials. One member of the group, *Brewcria Pickeringii,* has very numerous long decumbent stems, forming an elevated mass at the center, and spreading out in all directions on the sand.

The shrubs of the association are for convenience classified in this group. They include *Rhus canadensis,* var. *illinoensis,* forming dense rounded masses 3-15 feet (1-5 m.) across and three feet (1 m.) high, and excluding all other vegetation; *Amorpha canescens* and *Ceanothus americanus,* undershrubs with several erect or ascending stems one to three feet (3-8 dm.) high; and *Ceanothus ovatus* (Pl. II, Fig. 2), with several ascending stems forming an irregular bushy shrub two or three feet (1 m.) tall. The two species of *Ceanothus* are notable for their immense woody roots, frequently six inches (1.5 dm.) in diameter and extending downward to great depths. They are crowned by a few live stems, which are of comparatively short life, and with the dead and decaying bases of many others of previous years.

It is needless to say that the vast majority of these plants present obvious xerophytic adaptations, the most general of which are a reduction of surface to narrow or small leaves, and a protective covering of silvery or canescent hairs or scales. Their general tone is grayish green, amid which the vivid green of *Euphorbia corollata* and *Tradescantia reflexa* appears strangely out of place. The various types described do not include all the species of the group, but omit some of the less frequent. Neither do all perennials belong to this

group, but some, as *Lesquerella argentea,* are placed among the interstitials.

The second group includes the mat-plants, a small group with but three flowering plants, *Opuntia Rafinesquii, Opuntia fragilis,* and *Antennaria* sp. *Selaginella rupestris* is also common in the Hanover area. These grow close to the sand and tend to spread annually over a larger area. They are unable to encroach upon either the bunch-grasses or the perennials, and do not survive when covered by members of these groups. Their number is accordingly largest in the more open consocies. These plants are of the greatest importance in binding sand, and under certain conditions have a prominent part in stabilizing blowing sand. *Selaginella rupestris* is especially noteworthy for its habit of circular growth. Extending vegetatively from the center, its growth is so regular that a circular patch is formed. This is soon converted into a ring by the death of the center, leaving a marginal zone of living plants one to two inches (2-5 cm.) wide. This ring gradually increases in size until it may reach a maximum diameter of four feet (1.2 m.). Additional rings may begin within an old one, or parts of two rings may overlap. Megaspores are produced in enormous quantities, but their successful growth must be rare. The prickly pear, *Opuntia Rafinesquii,* is much more common in the Havana area than in any of the others. The mats of *Selaginella* are favorite places for small mats of a dark colored crusty species of *Cladonia.* Small mosses, of unidentified species, are also frequently found, and in many places a dark-colored crust on the sand is formed by a species of *Oscillatoria,* which from its habit may also be classified with the mats.

The third group, the interstitials, is composed in general of annuals, with slender, frequently unbranched stems, generally narrow leaves, and fibrous roots. They come up late, principally during the season of heavy rainfall in June or July, and cover the bare areas of sand with prodigious numbers of individuals. Notwithstanding their number, they are of the least ecological importance. Their slender stems occupy little space and take no part in sand-binding, while the very existence of the entire group is due to the presence of the bunch-grasses, which act as windbreaks and hold the sand. If the number of grasses decreases somewhat, there is a correspondingly larger number of interstitials, but if the bare spots become too large, so that blowing of the sand begins, their number begins to decrease.

The most abundant species of interstitials are *Oenothera rhombipetala, Ambrosia psilostachya, Linaria canadensis, Cassia Chamaechrista, Monarda punctata,* and *Croton glandulosus,* var. *septentrionalis.*

The fourth group, or parasites, is represented by a single species of seed plant, *Orobanche fasciculata,* found on the roots of *Artemisia caudata* in the Hanover area.

While these four groups are sufficiently distinct to serve as ecological units, they are not absolutely separate. The perennial *Lespedeza capitata,* with its slender stems and narrow leaves, associates frequently with the true interstitials, and might then well be regarded as one of them. *Cyperus Schweinitzii* appears now as a bunch-grass, now as an interstitial. *Bouteloua hirsuta* behaves sometimes as a bunch-grass, producing small tufts two to four inches (5-10 cm.) high, but frequently it functions more as a mat and associates with *Selaginella rupestris* and *Antennaria* sp., or, when growing between larger bunches of *Koeleria cristata,* it might be regarded also as an interstitial.

The number of secondary species and individuals is naturally greatest in the more open parts of the association and least in the denser portions. The mats may entirely disappear and the interstitials be greatly reduced in number when the bunch-grasses are closely aggregated. The perennials, with their greater resistance to crowding by the grasses, remain throughout and always occupy a prominent place in the association. The close relation between the secondary and dominant plants of an association is seldom better illustrated than in this one, where the presence and disappearance of the interstitials are both correlated with the density and luxuriance of the bunch-grasses.

The association as a whole is, as already noted, divided into a number of consocies. Some of these are characterized by a single species of grass and may be called pure consocies. Such are those characterized by *Koeleria cristata, Leptoloma cognatum, Stipa spartea,* and *Carex Muhlenbergii.* A larger part of the association is occupied by several characteristic species and is here termed the mixed consocies. Although the specific composition of the latter varies somewhat from place to place, its general appearance is so uniform that it does not admit of further subdivision. Besides describing these five, representing natural conditions, it is necessary also to mention some of the effects of cultivation, pasturing, and burning. The consocies are described in the reverse order of their importance, and the notes on cultural changes follow. It will be observed that the floristic differences between the various consocies are slight.

The Carex Muhlenbergii Consocies

The only observed examples of this consocies were in the Hanover area, the first in an interdunal depression, the second on the

side of a gentle slope. In both cases they were surrounded by other consocies of the same association, but were sharply separated from them.

The dominant species is *Carex Muhlenbergii*. The bunches are separate or rarely confluent and cover about three fourths of the surface. Since there are few dead leaves beneath the bunches, and the living leaves are mainly erect, there is abundant space for other plants. Although four species of grasses are included, of which three are typical bunch-grasses, they are so sparsely represented that none can at any place be considered dominant. The following secondary species were noted.

Bunch-grasses:

Leptoloma cognatum
Panicum virgatum
Panicum pseudopubescens
Poa pratensis

Perennials:

Lithospermum Gmelini
Pentstemon hirsutus
Solidago nemoralis
Helianthus scaberrimus
Helianthus occidentalis

Mat:

Opuntia Rafinesquii

Interstitials:

Monarda punctata
Linaria canadensis
Ambrosia psilostachya
Lactuca canadensis

The vernal aspect is characterized by *Lithospermum Gmelini*, the serotinal by *Monarda punctata*, and the autumnal by *Helianthus occidentalis*. The whole consocies stands out in sharp relief from its surroundings because of the rich dark-green color of the dominant species.

Carex Muhlenbergii is also widely distributed throughout the bunch-grass association, and occasionally appears in large numbers on the lee deposits of blowouts, and may take part in their stabilization. That the consocies does not have this origin is shown by the absence of *Diodia teres* and *Tephrosia virginiana*, the poor development of *Panicum virgatum*, and the presence of *Opuntia Rafinesquii*.

The Stipa spartea Consocies

This consocies is developed in but one place in the Hanover area, and is there of limited extent.

Stipa spartea is the dominant grass, with *Poa pratensis* second in abundance. The bunches of *Stipa* are here more or less confluent, and the intervening spaces are so occupied by blue-grass that the surface of the sand is completely covered. This leaves no opportunity for the growth of the usual interstitial plants and also tends to limit the number of perennials. But four species occur and they are represented by few individuals. They are *Panicum pseudopubescens*, *Callirhoe triangulata*, *Coreopsis palmata*, and *Aster linariifolius*. All of these are common in other consocies of the same association.

At either side the consocies changes rather abruptly into another characterized by *Koeleria cristata*, which has larger open spaces between the bunches and permits the growth of more secondary species.

The Koeleria cristata Consocies

In the Hanover area this is by far the most important consocies of the bunch-grass association which is characterized by a single species, and in area is second only to the mixed consocies. If its present extent may be taken as an index, it must originally have covered hundreds of acres of the sand prairie, although in scattered patches of rather small size. It is found alike on the sides and tops of the hills, but seldom in the depressions between them. Elsewhere the consocies was not observed.

The dominant species is *Koeleria cristata*. The bunches of this grass are mostly separate and compact, occupying from one half to two thirds of the surface. The dead basal leaves cover the sand between the bunches, and make an efficient protection against blowing. *Panicum pseudopubescens*, which flourishes where the sand is largely bare, is also frequently well developed.

The number of secondary plants is large because of the unusual amount of ground space available, and comparatively many species are represented. The number of individuals of the interstitial species is especially large. The mats of *Selaginella rupestris* reach here their maximum size; regular circles up to three feet (1 m.) in diameter are common, and they may become confluent to form solid masses eight to ten feet (2-3 m.) wide. *Koeleria cristata* lives indiscriminately upon these mats or between them, and so do most of the perennials. *Panicum pseudopubescens* and the annuals are seldom found except on the bare sand between them. The centers of the *Selaginella* mats are usually covered with a black crust, upon which a species of *Cladonia* is frequently growing. *Antennaria* sp. may grow on the mats also, or in the absence of *Selaginella* form

circular patches one to three feet (3-10 dm.) across, which are very conspicuous because of their gray color. The principal secondary species are the following.

Bunch-grasses:

Sorghastrum nutans
Panicum virgatum
Panicum pseudopubescens
Panicum perlongum
Stipa spartea

Perennials:

Tradescantia reflexa
Amorpha canescens
Petalostemum candidum
Petalostemum purpureum
Tephrosia virginiana
Viola pedata
Callirhoe triangulata
Lithospermum Gmelini
Pentstemon hirsutus
Solidago nemoralis
Aster sericeus
Aster linariifolius
Helianthus scaberrimus
Coreopsis palmata
Artemisia caudata

Mats:

Selaginella rupestris
Opuntia Rafinesquii
Opuntia fragilis
Antennaria sp.

Interstitials:

Festuca octoflora
Rumex Acetosella
Lepidium virginicum
Arabis lyrata
Oxalis corniculata
Scutellaria parvula
Monarda punctata
Ambrosia psilostachya

The vernal aspect is characterized by the blue flowers of *Viola pedata*, which were still in bloom when the consocies was first visited in June; later, *Pentstemon hirsutus* and *Lithospermum Gmelini* are conspicuous with their white and yellow flowers. The aestival season is well markd by *Tradescantia reflexa*, and the serotinal by *Monarda punctata*, which is frequently present in immense numbers. The flowers of the prairie clovers (*Petalostemum*), the lead plant (*Amorpha canescens*), and the sand poppy (*Callirhoe*) appear at the same season, but the plants are usually too scattered to break the effect of the masses of *Monarda*. Still later, in the autumnal aspect, the prevailing tone is yellow from the flowers of the goldenrod, *Solidago nemoralis*.

The *Koeleria cristata* consocies illustrates well the general principle that an association may be derived from different sources. In

some cases it is evidently the result of the stabilization of the *Panicum pseudopubescens* association, in which event it is characterized by the greater abundance of that species, the better development of mats, which are composed of *Selaginella* rather than *Antennaria,* and the greater abundance of *Scutellaria parvula* and *Arabis lyrata.* In other cases it is entirely independent of any former blow conditions, and then contains less *Panicum pseudopubescens,* mats of *Antennaria* rather than *Selaginella,* and a larger proportion of perennials, including *Aster sericeus* and *Amorpha canescens,* which are absent on blowing sand. The two types have the same structure and represent the same consocies, notwithstanding their difference in species. The only ecological difference between them, aside from their origin, is their age, and it may very properly be considered that the floral difference will gradually disappear as the various perennials succeed in establishing themselves in the younger type. The order of appearance of the species in this process of stabilization will be considered later.

There is usually a gradual change in the appearance of the consocies at its margin as other grasses appear or as *Koeleria* disappears. The secondary species vary but little specifically, but the number of individuals naturally increases or decreases according to the density of the grasses.

The Leptoloma cognatum Consocies

This consocies is extensively developed in the Hanover, the Dixon, and the Oquawka areas, and in the last two is by far the most important consocies characterized by a single species (Pl. I, Fig. 2). In the Hanover area it is exceeded in extent by the *Koeleria cristata* and the mixed consocies. It has a wider topographic range than the *Koeleria cristata* consocies, and is found in the interdunal depressions as well as on the hilltops.

Leptoloma cognatum is the principal bunch-forming grass, and its flat-topped bunches are usually so confluent that nine tenths of the surface or more is occupied. The bunches are of such uniform height and density that the consocies appears as if artificially trimmed, and has a generally gray-green color because of the numerous dead leaves mixed with the living. The other grasses, which are usually of larger size and bright green in color, stand out very prominently against the background. In the serotinal aspect the plants are in bloom, and the large panicles with the red spikelets are so numerous that the whole consocies has a reddish hue. A few other grasses may at some places occupy enough of the surface to affect the general appearance of the consocies. They are *Koeleria cristata* at Han-

over and Dixon, *Sorghastrum nutans* at Hanover, *Panicum pseudopubescens* at Hanover, *Andropogon scoparius* at Dixon and Oquawka, and *Paspalum setaceum* at Oquawka. At Dixon, *Chrysopsis villosa* becomes conspicuous and occupies a large amount of space, but it seems probable that the conditions there are not quite normal.

It has already been noted that the confluent habit of the bunches of *Leptoloma cognatum* restricts the space for secondary species. The great extent of the consocies, on the other hand, tends to increase the number of species, even though the number of individuals is relatively small. A list of the secondary species follows.

Bunch-grasses:

Andropogon scoparius
Sorghastrum nutans
Paspalum setaceum
Panicum perlongum
Panicum Scribnerianum
Panicum pseudopubescens
Koeleria cristata
Bouteloua hirsuta
Bouteloua curtipendula
Poa pratensis
Cyperus Schweinitzii
Carex umbellata
Carex Muhlenbergii

Perennials:

Tradescantia reflexa
Sisyrinchium sp.
Oxybaphus nyctagineus
Delphinium Penardi
Baptisia bracteata
Amorpha canescens
Petalostemum purpureum
Tephrosia virginiana
Lespedeza capitata
Polygala polygama
Euphorbia corollata
Rhus canadensis, var. *illinoensis*
Ceanothus americanus
Callirhoe triangulata
Helianthemum majus
Viola pedata.
Asclepias amplexicaulis
Acerates viridiflora
Acerates viridiflora, var. *lanceolata*
Lithospermum Gmelini
Verbena stricta
Verbascum Thapsus
Pentstemon hirsutus
Ruellia ciliosa
Liatris scariosa
Chrysopsis villosa
Solidago speciosa, var. *angustata*
Solidago nemoralis
Aster linariifolius
Helianthus scaberrimus
Achillea Millefolium

Mats:

Selaginella rupestris
Opuntia Rafinesquii
Antennaria sp.
Senecio Balsamitae

Interstitials:

Festuca octoflora
Cyperus filiculmis
Rumex Acetosella
Polygonum tenue
Silene antirrhina
Arabis lyrata
Lepidium virginicum
Cassia Chamaechrista
Linum sulcatum
Polygala incarnata
Croton glandulosus, var. *septentrionalis*
Oenothera rhombipetala
Monarda punctata
Hedeoma hispida
Linaria canadensis
Specularia perfoliata
Erigeron annuus
Erigeron ramosus
Ambrosia psilostachya

Of the grasses in the above list, *Boutcloua hirsuta* is most abundant in the Oquawka area, and may usually be found in any of the narrow strips of sand between the bunches of *Leptoloma*, although its small size makes it very inconspicuous. Near Hanover, *Boutcloua* does not occur in this consocies, and *Panicum Scribnerianum* and *Panicum perlongum* are important secondary species. The others are usually infrequent but are sometimes very conspicuous if the bunches are of large size and overtop the *Leptoloma*. Those of *Andropogon scoparius* and *Carex Muhlenbergii* contrast especially with *Leptoloma* both in size and color.

In the Hanover area the most abundant perennials are *Euphorbia corollata* and *Helianthus scaberrimus*; in the Oquawka area, *Ruellia ciliosa* and *Baptisia bracteata*. Many of the perennials are conspicuously taller than the *Leptoloma* and stand out in prominent relief above it. This is especially true of the bushy shrubs *Ceanothus americanus*, *Rhus canadensis*, var. *illinoensis*, and *Amorpha canescens*.

Antennaria is the most abundant mat, and is frequent throughout the consocies. The mats are small because of the limited space available. *Senecio Balsamitae* forms dense patches two to three feet (5-10 dm.) across and shows some tendency to resist the encroachment of the bunch-grasses.

Of the interstitial plants, *Ambrosia psilostachya* is omnipresent, and is represented by an immense number of individuals. *Rumex Acetosella* and *Monarda punctata* are also very abundant. The latter is one of the most conspicuous features of the serotinal aspect. *Oenothera rhombipetala* is not so abundant as *Monarda*, but is equally conspicuous at its blooming season during the aestival aspect, because of its taller stems and vivid yellow flowers. The other interstitial plants vary greatly from place to place, and almost any

species may in some places or at some seasons appear very conspicuously. A striking example of this was given by *Linum sulcatum,* which was observed only on one sand-hill near Oquawka, and was so local that it did not appear in any of the quantitative studies made there. The plant has very slender erect unbranched stems, and during the first days of July was hardly noticeable. A few days later the flowers appeared and brought the plant at once so much into evidence that it might have been wrongly considered a characteristic member of the consocies.

TABLE I.—FLORISTIC COMPOSITION OF TEN QUADRATS IN THE *Leptoloma cognatum* CONSOCIES, OQUAWKA AREA.

Leptoloma cognatum	X	X	X	X	X	X	X	X	X	X
Paspalum setaceum	X	X	-	X	X	X	-	X	X	-
Panicum Scribnerianum	-	X	-	-	-	X	X	-	-	-
Bouteloua hirsuta	X	X	-	X	X	X	-	X	X	X
Cyperus filiculmis	-	-	-	-	-	-	-	X	X	-
Carex Muhlenbergii	-	-	-	-	-	-	-	-	X	-
Rumex Acetosella	-	X	X	X	X	-	X	X	X	X
Polygonum tenue	-	-	-	-	-	X	-	-	-	X
Silene antirrhina	-	-	X	-	-	-	X	-	-	-
Cassia Chamaechrista	-	X	X	X	-	-	X	X	-	-
Baptisia bracteata	X	X	X	-	X	-	-	X	-	X
Amorpha canescens	-	X	X	-	X	-	-	-	-	X
Polygala incarnata	X	-	-	-	-	-	-	-	-	-
Oenothera rhombipetala	-	-	-	X	-	-	X	-	-	X
Verbena stricta	X	X	-	X	-	-	X	X	X	-
Monarda punctata	X	-	X	X	-	X	X	-	-	X
Hedeoma hispida	-	-	-	-	-	-	X	-	X	-
Linaria canadensis	-	-	X	-	-	-	-	-	-	-
Pentstemon hirsutus	-	-	-	-	-	X	-	-	X	-
Ruellia ciliosa	X	X	X	X	X	X	X	X	X	X
Specularia perfoliata	-	X	-	-	-	-	-	-	-	-
Erigeron ramosus	-	-	-	X	X	X	X	-	-	X
Antennaria sp.	-	X	-	-	-	-	-	-	-	-
Ambrosia psilostachya	X	X	-	X	X	X	X	X	X	X
Senecio Balsamitae	-	-	-	-	-	-	X	-	-	-

A series of counts (Table I) were made at Oquawka, in the best example of the consocies observed (near the site of Plate I, Fig. 2), to determine the relative frequency of the secondary species. These counts record the presence or absence of the species in each of ten quadrats two meters square, extending in a continuous strip through

the consocies. No record was made concerning the abundance of each species.

Boutelona hirsuta, Ruellia ciliosa, Ambrosia psilostachya, and *Rumex Acetosella* appear as the most frequent of the secondary species, while *Leptoloma cognatum* naturally appears in every quadrat. The average number of species in each quadrat is 10.6, while the whole number observed in the Oquawka area is 47.

The consocies was not under observation during the vernal season, but *Baptisia bracteata* and *Delphinium Penardi* are probably quite conspicuous at that time. During the aestival aspect of late June and July *Oenothera rhombipetala* and *Amorpha canescens* are much in evidence. These are followed in August by *Monarda punctata,* and the red spikelets of *Leptoloma cognatum* are also very conspicuous at that season. In the Hanover area the vernal aspect is characterized by *Pentstemon hirsutus,* while the aestival and serotinal conditions are essentially the same as at Oquawka.

In the Oquawka area contact between this consocies and others was not observed. At Hanover it grades into the mixed consocies next to be described. There is no sharp line between the two, but other species of grasses appear, the spaces between the bunches become wider, and a greater number of secondary species occupy the bare sand thus available.

The Mixed Consocies

In the Hanover area the greatest portion of the sand prairie was originally occupied by a mixed consocies, in which several species of bunch-grass were well represented (Pl. II; Pl. III, Fig. 1). The same consocies was also of considerable importance in the Havana area, and was described in a former paper (Hart and Gleason, *1907:* 158-160). It was also well represented in the Oquawka area, especially in the prairies between Keithsburg and Oquawka. In the Dixon area no estimate can be made at present concerning its former extent. It seems probable that over the sand prairies as a whole at least two thirds of the surface was occupied by this mixed growth. Although now greatly reduced in area because of cultivation, the remnants left show that it grew alike on the higher elevations and on the depressions between the hills; that there was little difference in the vegetation as the habitat changed; and that the specific composition of the grasses varied considerably from place to place, but that the general appearance of the consocies was remarkably uniform.

The reason for its wide extent is obvious. The bunch-grasses all belong to the same ecological type, and, with the unimportant exception of *Bouteloua hirsuta,* have approximately the same size. Competition between them therefore is largely limited to a struggle for ground space, and of that there is usually an abundance. There is very little possibility of one species shutting off the light from another, either by its size or by making an earlier start in the season. The dead leaves and culms with which each bunch is surrounded make a good ground cover which holds the sand and excludes the growth of seedlings of competing species. None of the species is distinguished by a particularly large seed production or by special adaptations for seed dispersal. Few of them spread by underground stems. Taking all these points into consideration, it is clear that there are no particular adaptations which might lead to a monopoly by one species in the consocies. The presence of so many species indiscriminately mixed is caused by their uniform dissemination and continued by the evenness of their competition for space. For a few species these statements do not hold. The small bunches of *Bouteloua hirsuta* and the flat ones of *Panicum pseudopubsccns* are easily overshadowed and killed by the growth of other species. The loose, few-leaved bunches of *Stipa spartea* similarly tend to be crowded out by species of denser habit. These three species, accordingly, are not to be found throughout the consocies, but tend to disappear as the surface becomes more completely covered.

The number of grasses which occur is large, and includes virtually every species of bunch-grass found in the region. Not all of them occur together, or even in the same area, but in most places three or four may be recognized as of chief importance, while the others have more of the nature of secondary species. The following bunch-grasses were observed:

**Andropogon scoparius*
**Andropogon furcatus*
Sorghastrum nutans
**Leptoloma cognatum*
Paspalum setaceum
**Panicum virgatum*
Panicum perlongum
Panicum Scribnerianum
**Panicum pseudopubescens*
**Stipa spartea*
Calamovilfa longifolia
**Koeleria cristata*
**Bouteloua hirsuta*
**Bouteloua curtipendula*
Eragrostis trichodes
**Eragrostis pectinacea*
Poa pratensis
**Cyperus Schweinitzii*
Carex umbellata
Carex Muhlenbergii

Of these twenty species, eleven, marked with an asterisk, have been noted in some locality as dominant species, that is, so abundant

and occupying so much space that their removal would seriously change the nature and appearance of the consocies. A further study shows that three species are so regularly present and so frequently associated with each other that they may be regarded as the most typical grasses of the consocies. They are *Leptoloma cognatum*, *Koeleria cristata*, and *Andropogon scoparius*. The remaining nine grasses are always secondary species and never occupy a considerable portion of the ground space. Their huge bunches, as of *Sorghastrum nutans*, or tall culms, as of *Calamovilfa longifolia*, may nevertheless make them very conspicuous in some places. A few other grasses, not bunch-formers, are also mentioned under the proper head.

There is a great variety of perennials, interstitials, and a few mats, of which the following were listed.

Perennials:

Equisetum hyemale, var. *intermedium*
Tradescantia reflexa
Sisyrinchium sp.
Anemone cylindrica
Baptisia bracteata
Amorpha canescens
Petalostemum purpureum
Petalostemum candidum
Tephrosia virginiana
Lespedeza capitata
Polygala polygama
Euphorbia corollata
Rhus canadensis, var. *illinoensis*
Ceanothus americanus
Ceanothus ovatus
Callirhoe triangulata
Helianthemum majus
Viola pedata
Asclepias amplexicaulis
Acerates viridiflora
Acerates viridiflora, var. *lanceolata*
Brewcria Pickeringii
Phlox bifida
Lithospermum Gmelini
Verbena stricta
Physostegia dentieulata
Physalis virginiana
Physalis heterophylla
Pentstemon grandiflorus
Pentstemon hirsutus
Synthyris Bullii
Kuhnia eupatorioides, var. *corymbulosa*
Liatris cylindracea
Liatris scariosa
Chrysopsis villosa
Solidago speciosa, var. *angustata*
Solidago nemoralis
Solidago missouriensis
Solidago rigida
Aster sericeus
Aster multiflorus
Aster linariifolius
Aster sp.
Brauneria pallida
Helianthus scaberrimus
Helianthus occidentalis
Coreopsis palmata
Achillea Millefolium
Artemisia caudata

Interstitials:

Aristida tuberculosa
Festuca octoflora
Elymus virginicus
Cyperus filiculmis
Stenophyllus capillaris
Carex pennsylvanica
Carex festucacea, var. *brevior*
Commelina virginica
Polygonum tenue
Chenopodium album
Froelichia floridana
Mollugo verticillata
Silene antirrhina
Talinum rugospermum
Lesquerella argentea
Lepidium virginicum
Erysimum parviflorum
Arabis lyrata
Cassia Chamaecbrista
Strophostyles sp.
Linum sulcatum
Polygala verticillata
Croton glandulosus, var. *septentrionalis*
Crotonopsis linearis
Euphorbia Geyeri
Oenothera rhombipetala
Verbena bracteosa
Monarda punctata
Hedeoma hispida
Linaria canadensis
Specularia perfoliata
Erigeron ramosus
Erigeron canadensis
Gnaphalium polycephalum
Ambrosia psilostachya
Lactuca canadensis

Mats:

Selaginella rupestris
Opuntia Rafinesquii
Antennaria sp.

Parasite:

Orobanche fasciculata

Not every station of the consocies contains all of these secondary species, or even a majority of them. The actual specific composition of the consocies and the frequence and abundance of the species vary so greatly from place to place that individual descriptions must be given. Seven distinct areas occupied by the mixed consocies were examined with more or less detail.

1. Hanover area, one mile southwest of the railway station. The consocies occupies a flat interdunal depression (Pl. III, Fig. 1). Nine species of bunch-grasses are present, which are named in the approximate order of their abundance: *Leptoloma cognatum*, *Koeleria cristata*, *Stipa spartea*, *Sorghastrum nutans*, *Panicum perlongum*, *Panicum Scribnerianum*, *Carex Muhlenbergii*, *Panicum pseudopubescens*, and *Bouteloua hirsuta*. Of these the first two occupy more space than the other seven together. The bunches are very compact and close and at a little distance resemble a close sod. Many dead leaves

collect under the bunches, aiding in the soil formation, and even the narrow strips between the bunches are frequently covered with dead leaves. On the small open spots are mats of *Antennaria* sp. and *Selaginella rupestris,* often growing together, and as the *Selaginella* dies out in the middle of the mats a brownish moss comes in. The result is that there is absolutely no chance for the sand to blow and humus can form rapidly. The surface sand is dark brown in color, somewhat loamy in texture, and partially coherent because of the mass of rootlets in it. This condition continues to a depth exceeding ten inches (25 cm.). Of the grasses mentioned, *Panicum pseudopubescens,* often so abundant in the consocies, is quite scarce, because of the absence of flat bare sand areas on which its decumbent bunches may spread. *Boutcloua hirsuta* is also scarce for the same reason. It grows in small tufts two to four inches (5-10 cm.) high on the mats of *Selaginella.* The presence of *Panicum Scribnerianum* is of interest, since it occurs only in the densest growth of bunchgrass. Thirty-one secondary species occur in various degrees of frequency. Ten quadrats of four square meters each were examined, and the numeral following each plant name indicates the number of quadrats in which the species occurred. Eleven species, without numbers, did not appear in the quadrats, but were found elsewhere in the consocies. The secondary species are as follows.

Perennials:

Equisetum hyemale, var. *intermedium* (2)
Poa pratensis
Petalostemum purpureum (1)
Tephrosia virginiana (4)
Polygala polygama
Euphorbia corollata (4)
Viola pedata (1)
Callirhoe triangulata (7)
Lithospermum Gmelini (2)
Acerates viridiflora, var. *lanceolata* (1)
Physalis virginiana
Aster sericeus (1)
Aster linariifolius (8)
Aster sp.
Helianthus scaberrimus (6)
Coreopsis palmata (2)
Artemisia caudata (1)

Mats:

Selaginella rupestris (8)
Opuntia Rafinesquii (1)
Antennaria sp. (6)

Interstitials:

Festuca octoflora
Chenopodium album
Arabis lyrata (1)
Hedeoma hispida
Linaria canadensis
Specularia perfoliata

Oenothera rhombipetala (1) *Erigeron ramosus*
Verbena bracteosa *Ambrosia psilostachya* (9)
Monarda punctata (4)

It may be noticed that of the twenty species appearing in the quadrats only four were interstitials, while of the eleven more infrequent species not appearing in the quadrats seven were interstitials. The relative frequency of the perennials is as 172 to 100. This illustrates and substantiates the general principle that the number of individuals of interstitial plants decreases as the density of the bunchgrass increases. Although *Ambrosia psilostachya* has a greater frequency than any of the perennials, it actually plays a very unimportant part in the consocies. Growing up straight and slender, it is quite inconspicuous and really much less important than *Aster linariifolius*. The high frequency of the latter species and of *Callirhoe triangulata* is also of interest

2. Hanover area; up the hill (Pl. III, Fig. 1) toward the plateau at the southwest of the station just described. The consocies continues without interruption, but is somewhat different in appearance (Pl. II, Figs. 1, 2). On the hillside the dominant species are the same, but *Panicum Scribnerianum* and *Selaginella rupestris* disappear; the mats of *Antennaria* are sparse; the ground is not well covered and does not have the loamy texture of the sand in the depression. *Boutelona hirsuta* becomes more abundant, corresponding to the larger surface of open sand, and *Linaria canadensis*, an interstitial, is common with it. The remaining secondary species are almost the same as in the valley. A transect up this hillside is shown in Table II. The table shows that the change from the lower (left) end of the transect to the upper is caused chiefly by the addition of species as the space between the bunches becomes larger. In the first half the average number of species per quadrat of 0.25 sq. m. is 2.5, while in the last half it is increased to 4.35.

TABLE II.—TRANSECT OF 40 QUADRATS, EACH 5 DM. SQUARE, THROUGH THE MIXED CONSOCIES, HANOVER AREA.

Selaginella rupestris	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Andropogon scoparius	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	X	-	-	X	X	-	X	-	-	-	X	X	X	X	X	-	X	X	X	-	-	-
Sorghastrum nutans	-	-	-	-	-	-	-	-	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptoloma cognatum	X	X	X	X	X	X	X	X	-	X	X	X	X	X	X	X	X	-	-	X	X	-	X	-	-	-	X	X	X	-	X	X	-	X	-	X	X	-	-	-
Panicum perlongum	X	-	-	-	-	X	X	-	-	X	-	-	X	-	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-	-
Panicum pseudopubescens	-	-	-	-	-	-	X	-	-	-	-	-	-	X	X	X	-	X	-	X	X	-	-	-	-	-	-	-	-	-	-	-	X	X	X	-	-	X	X	X
Bouteloua hirsuta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	X	X	X	-	X	-	-	X	-	X
Koeleria cristata	-	-	-	X	-	-	-	-	X	-	-	-	-	-	X	X	-	-	-	X	X	X	X	-	X	-	X	-	X	-	-	-	-	-	X	-	-	X	-	X
Festuca octoflora	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	X	-	-	-	-	-	-	-	X
Carex umbellata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X
Talinum rugospermum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Arabis lyrata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Petalostemum purpureum	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbia corollata	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Callirhoe triangulata	X	-	X	-	-	-	-	-	-	-	-	X	X	-	-	-	X	-	-	-	X	X	-	X	X	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-
Oenothera rhombipetala	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Monarda punctata	-	-	-	-	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Linaria canadensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	X	-	X	-	X
Solidago nemoralis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-	-	-	-	-
Aster linariifolius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	-	X	X	X	X	X	X	X	X	-	X	-
Antennaria sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ambrosia psilostachya	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	X	-	-	-	-	X	X	X	-	-
Helianthus scaberrimus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-

On the top of the hill there is again a little *Selaginella,* but the areas between the bunches are mostly bare or with *Boutcloua,* here growing in short flat irregular tufts. *Andropogon scoparius* appears in great abundance and becomes the most conspicuous member of the consocies. Frequency counts were made here also, as indicated by the numerals following the names. The ten bunchgrasses present are as follows:

Andropogon scoparius (10)
Sorghastrum nutans
Leptoloma cognatum (7)
Panicum perlongum (1)
Panicum Scribnerianum
Panicum pseudopubescens (10)
Stipa spartea
Bouteloua hirsuta (10)
Koeleria cristata (10)
Carex Muhlenbergii

Of these *Andropogon scoparius, Leptoloma cognatum,* and *Koeleria cristata* are the most important and are almost equally abundant. The flat bunches of *Panicum pseudopubescens* are very numerous, but are inconspicuous among the larger bunches of the other taller grasses.

The ground is open, with probably 20 per cent. of the surface exposed. The intervening spaces are bare or sparsely covered with dead stems and leaves, or rarely with mats of *Selaginella.* This permits a larger development of *Panicum pseudopubescens* and the interstitial vegetation, and the counts show that six of the seven interstitials are frequent enough to appear in one or more of the plots. Although the location is on top of a hill there is no evidence of blowing. The secondary species are as follows.

Perennials:

Carex festucacea, var. *brevior*
Tradescantia reflexa
Petalostemum purpureum
Lespedeza capitata (1)
Euphorbia corollata (1)
Ceanothus ovatus
Callirhoe triangulata (4)
Helianthemum majus
Viola pedata
Acerates viridiflora, var. *lanceolata*
Lithospermum Gmelini (2)
Aster sericeus (3)
Aster linariifolius (6)
Solidago nemoralis (4)
Helianthus scaberrimus (4)
Coreopsis palmata
Artemisia caudata (1)

Mats:

Selaginella rupestris (1)
Opuntia Rafinesquii

Interstitials:

Festuca octoflora (1)
Arabis lyrata
Oenothera rhombipetala (1)
Monarda punctata (3)
Linaria canadensis (4)
Erigeron ramosus (1)
Ambrosia psilostachya (9)

The relative frequency of perennials and interstitials is 56 to 100.

3. Oquawka area; a small tract of bunch-grass near the station at Milroy. The dominant vegetation consists of four grasses, almost equally abundant: *Koeleria cristata*, *Andropogon furcatus*, *Boutelona curtipendula*, and *Boutelona hirsuta*. Four other grasses are also present: *Stipa spartea*, *Panicum pseudopubescens*, *Panicum Scribnerianum*, and *Andropogon scoparius*. Other secondary species are as follows.

Perennials:

Tradescantia reflexa
Tephrosia virginiana
Lespedeza capitata
Euphorbia corollata
Rhus canadensis, var. *illinoensis*
Acerates viridiflora
Pentstemon hirsutus
Liatris scariosa
Solidago speciosa, var. *angustata*
Solidago nemoralis
Helianthus scaberrimus
Corcopsis palmata

Mat:

Opuntia Rafinesquii

Interstitials:

Cyperus filiculmis
Froelichia floridana
Lepidium virginicum
Cassia Chamaechrista
Polygala verticillata
Croton glandulosus, var. *septentrionalis*
Monarda punctata
Linaria canadensis
Ambrosia psilostachya

The ground here is open and has probably been used at times for pasture. This accounts for the large number of interstitial plants present. The same consocies extends also along the railway right of way, where several additional species occur, including the following.

Bunch-grass:

Elymus canadensis

Perennials:

Carex pennsylvanica
Carex festucacea, var. *brevior*
Sisyrinchium sp.
Anemone cylindrica
Amorpha canescens
Ceanothus americanus
Helianthemum majus
Asclepias amplexicaulis
Brewcria Pickeringii
Verbena stricta
Physostegia denticulata
Pentstemon grandiflorus
Aster sericeus
Aster multiflorus
Brauneria pallida
Achillea Millefolium

Interstitials:

Stenophyllus capillaris
Commelina virginica
Polygonum tenue

4. Oquawka area; nearly original bunch-grass near the county line between Henderson and Mercer counties. The dominant species are *Andropogon scoparius, Koeleria cristata,* and *Leptoloma cognatum,* named in order of their abundance. These three species are mixed indiscriminately and with them are several other bunch-grasses of less importance in the consocies. These are *Panicum pseudopubescens, Panicum virgatum, Panicum Scribnerianum, Andropogon furcatus, Bouteloua hirsuta,* and *Carex Muhlenbergii.*

The ground is about 90 per cent. covered, and the spaces between the bunches are well covered with patches of moss, mats of *Antennaria,* and bunches of *Panicum pseudopubescens* and *Bouteloua hirsuta.* The secondary species are the following.

Perennials:

Tradescantia reflexa
Baptisia bracteata
Amorpha canescens
Tephrosia virginiana
Lespedeza capitata
Euphorbia corollata
Acerates viridiflora
Rhus canadensis, var. *illinoensis*
Physalis virginiana
Helianthus scaberrimus
Helianthus occidentalis
Brauneria pallida

Mat:

Antennaria sp.

Interstitials:

Paspalum setaceum
Cyperus filiculmis
Commelina virginica
Silene antirrhina
Cassia Chamaechrista
Oenothera rhombipetala
Monarda punctata
Linaria canadensis
Specularia perfoliata
Ambrosia psilostachya

During the aestival aspect the blue spikes of *Amorpha canescens,* the pink heads of *Brauneria pallida,* and the yellow flowers of *Oenothera rhombipetala* are very conspicuous. *Lespedeza capitata* is especially abundant near the railroad, where the ground has been somewhat disturbed.

5. Havana area; on "Tower Hill", four miles (6 km.) north of Topeka. *Leptoloma cognatum, Eragrostis pectinacea,* and *Bouteloua hirsuta* are the dominant species. These occupy about equal amounts of space, but the *Bouteloua* is of course relatively inconspicuous. Associated with the grasses are twelve secondary species, as follows.

Perennials:

Tephrosia virginiana
Callirhoe triangulata
Phlox bifida
Pentstemon hirsutus
Liatris scariosa
Aster sericeus
Aster linariifolius

Mats:

Opuntia Rafinesquii
Antennaria sp.

Interstitials:

Silene antirrhina
Lesquerella argentea
Cassia Chamaechrista
Crotonopsis linearis
Oenothera rhombipetala

6. Havana area; the "Devil's Neck", three miles (5 km.) north of Topeka. The bunches are rather widely scattered, leaving a considerable portion of the ground space exposed. They are formed by *Leptoloma cognatum, Cyperus Schweinitzii,* and *Panicum pseudopubescens.* The latter is most abundant in the more open spots, indicating the approach of blow conditions. But three species of perennials are present, *Tephrosia virginiana, Callirhoe triangulata,* and a few plants of *Lespedeza capitata.* Scattered mats of *Opuntia Rafinesquii* occur. The interstitial plants are numerous, corresponding to the large space available, and consist of *Aristida tuberculosa, Ambrosia psilostachya, Crotonopsis linearis, Commelina virginica, Oenothera rhombipetala, Mollugo verticillata, Cassia Chamaechrista,* and *Strophostyles helvola.* The consocies here represents the last stage before succession by the *Panicum pseudopubescens* association, and is probably also somewhat modified by pasturing.

7. Dixon area; in a field near the railroad. The ground is more or less carpeted with fine cinders discharged from locomotives. The vegetation consists of large bunches of *Andropogon furcatus,* with

smaller ones of *Andropogon scoparius, Panicum virgatum, Leptoloma cognatum,* and some *Paspalum setaceum.* Other less important species of bunch-grasses are *Stipa spartea, Cyperus Schweinitzii, Panicum pseudopubescens,* and *Koeleria cristata,* indicating a former luxuriant development of the consocies. There are also scattered plants of *Froelichia floridana, Monarda punctata, Liatris scariosa, Lithospermum Gmelini, Tephrosia virginiana,* and *Amorpha canescens.*

The aspect of the mixed consocies varies considerably from one area to another, but a few plants may be mentioned which are usually common and conspicuous. In the vernal aspect *Viola pedata, Pentstemon hirsutus,* and *Lithospermum Gmelini* are in bloom. They are followed during the aestival aspect of July by *Tradescantia reflexa, Chrysopsis villosa, Oenothera rhombipetala,* and *Amorpha canescens.* In the serotinal aspect *Solidago nemoralis, Liatris scariosa,* and a number of other composites appear. The consocies was not under observation during other aspects.

Cultural Changes

The railroads which traverse the sand areas make apparently little effort to keep the right of way free from tall grasses or other plants, and as a result fires occur frequently. Their chief effect seems to be to limit the growth of bunch-grasses to the largest species, and of those only the larger bunches are spared. The deposit of cinders along the track is also an important factor in the vegetation. It tends to increase the intensity of the xerophytic conditions, and hence to limit the plant growth. In this the greater heat absorption of the dark-colored, cindered surface may be controlling for the perennials, while the poorer chance of seed planting may tend to reduce the number of the annuals. The general effect of both fires and cinders is to increase greatly the amount of open space and to restrict the vegetation mainly to a few of the hardier species. There are of course frequent scattered relics of many other species of the association. An association of quite similar appearance, characterized by *Andropogon scoparius* and *Petalostemum purpureum,* appears on some of the gravelly ridges along Lake Michigan, where the surface of the ground is covered with flat rounded pebbles one to two inches (2-5 cm.) in diameter.

North of Oquawka, along the Chicago, Burlington and Quincy railroad there are many huge bunches of *Sorghastrum nutans, Andropogon furcatus,* and *Andropogon scoparius,* separated by interspaces 3-15 feet (1-5 m.) wide. Nearly all these bunches are dead in

the center, showing that they are of great age. But few perennials have persisted, the most notable of which is *Brewcria Pickeringii,* growing in large tangled masses three to five feet (1-2 m.) across.

Along the same railroad near Keithsburg, *Andropogon scoparius* is the dominant species. Burning there has been less frequent, or has not occurred for a longer time, since there are many plants of *Boutcloua hirsuta* and some blue-grass. *Antennaria* frequently forms mats on the ground and there are some patches of *Helianthus occidentalis,* which are so dense that almost all other plant growth is excluded from them. Some other perennials in this habitat are *Ceanothus americanus, Tradescantia reflexa, Solidago nemoralis, Desmodium illinoense,* and *Rudbeckia hirta,* but the most abundant of all is *Euphorbia corollata.* There are comparatively few interstitials.

Along the Chicago and Northwestern railroad southwest of Dixon the surface is thickly covered with cinders but there is little evidence of burning. There is a good growth of *Leptoloma cognatum,* and a few scattered plants of *Panicum Scribnerianum* still persist. *Euphorbia corollata* is abundant, and numerous patches of *Equisetum hyemale,* var. *intermedium* occur. Other secondary plants are *Chrysopsis villosa, Brauneria pallida, Helianthus occidentalis,* and *Monarda punctata.*

Pasturing, if too close, results in the destruction of part of the bunches and a consequent increase in the number of interstitials. If continued too long, the sand may begin to blow, ruining the pasture or possibly even the adjacent fields. The bunch-grasses seem to be poorly adapted to grazing and they are soon displaced by blue-grass. Some of the coarser species are avoided by stock, and persist for a longer time.

On a hillside pasture in the Hanover region *Eragrostis pectinacea* is in most places the only bunch-grass remaining. *Cyperus Schweinitzii* is abundant and blue-grass is appearing in a few patches. The secondary species include a large proportion of annuals, of which *Monarda punctata* is especially abundant. This species with its exceedingly pungent foliage is not eaten by stock and seems to flourish in pastures notwithstanding the tramping. It will be noted that many of the species listed below have a similar protection against grazing animals. The following species were observed.

Grasses:

Setaria glauca
Cenchrus carolinianus
Aristida tuberculosa
Eragrostis pectinacea
Poa pratensis
Cyperus Schweinitzii

Perennials:

Petalostemum purpureum
Petalostemum candidum
Euphorbia corollata
Callirhoe triangulata
Vernonia fasciculata
Liatris cylindracea
Liatris scariosa
Solidago nemoralis
Solidago rigida
Helianthus scaberrimus
Helianthus occidentalis
Artemisia caudata

Interstitials (excluding grasses):

Polygonum tenue
Mollugo verticillata
Draba caroliniana
Arabis lyrata
Polanisia graveolens
Linum sulcatum
Croton glandulosus, var. *septentrionalis*
Euphorbia Geyeri
Oenothera rhombipetala
Monarda punctata
Erigeron ramosus

Arabis lyrata is here sometimes very abundant and covers areas five to fifteen feet (2-5 m.) across to the exclusion of almost all other vegetation. These spots are always covered by gravel sorted out by water action, affording an optimum habitat for the rock-loving plant.

In the Oquawka area *Paspalum setaceum* and blue-grass tend to replace the bunch-grasses. The number of interstitials is increased, and *Monarda punctata, Erigeron ramosus,* and *Ambrosia psilostachya* become especially abundant. A few weedy perennials also remain, such as *Lactuca canadensis* and *Verbena stricta.*

Many of the roads across the sand prairies are little used and the roadsides are occupied by a vegetation very similar to the original bunch-grass. This is particularly true in the Hanover area, which is very sparsely settled. Even there *Poa pratensis* comes in and partially converts the bunch-grass into sod. Thickets of *Ribes gracile* and other berry-bearing shrubs come up along the fence-rows, and their shade is a favorite habitat for *Artemisia ludoviciana.* Various interstitials, especially *Cassia Chamaechrista, Digitaria filiformis, Mollugo verticillata,* and *Cenchrus carolinianus* grow even in the road-bed between the wheel-tracks.

The same general conditions obtain in the Havana and Oquawka areas, but with more travel because of the denser population the original bunch-grass is destroyed or obscured by the numerous weeds that follow civilization. These include two groups, the first composed of species normal to natural associations but flourishing also along the roadsides, and the second of true weeds, mostly natives of the Old World and not found on natural sand associations in the vicinity.

In the first group are *Verbena stricta, Strophostyles helvola, Monarda punctata, Froelichia floridana, Oenothera rhombipetala,* and *Lepidium virginicum.* The second is represented by *Digitaria filiformis, Trifolium pratense, Trifolium repens, Poa pratensis, Verbascum Thapsus, Hordeum pusillum, Anthemis Cotula, Erigeron canadensis, Polygonum erectum, Polygonum aviculare, Achillea Millefolium, Plantago Rugelii,* and *Chenopodium album.*

In the Oquawka area *Populus alba, Gleditsia triacanthos,* and *Robinia Pseudo-Acacia* are frequently planted along the roadsides, and shelter a number of more mesophytic species, such as *Solanum nigrum* and *Phytolacca decandra.*

In cultivated fields the weeds are composed mainly of introduced species and of those natives of the original bunch-grass which are readily propagated by seeds, thus including most of the interstitials and but few of the perennials. In the Hanover area the most abundant are *Lepidium virginicum* and *Rumex Acetosella.* Under certain conditions which could not be determined *Euphorbia corollata* and *Pentstemon hirsutus* come up in great abundance in almost pure association. A square meter taken at random contained 605 plants of the former species, and *Pentstemon* grows almost as densely. Other abundant weeds are *Monarda punctata, Hedeoma hispida, Silene antirrhina, Specularia perfoliata,* and *Diodia teres.* In the Havana area, where the prickly-pear, *Opuntia Rafinesquii,* is common, it frequently becomes a bad weed in corn fields. Cultivation does not kill it, but merely serves to break the plant up into joints and scatter it over a wider area. In the Oquawka area many fields are cultivated some years and abandoned others, and they always contain a heavy growth of weeds. One such field was almost carpeted with *Cenchrus carolinianus,* above which arose the yellow-flowered stalks of *Oenothera rhombipetala* in such numbers that from a distance the whole field looked yellow. The other weeds with them were *Mollugo verticillata, Strophostyles helvola, Polanisia graveolens, Ipomoea hederacea, Croton glandulosus,* var. *septentrionalis, Xanthium commune, Erigeron canadensis, Ambrosia artemisiaefolia, Solanum carolinense, Lepidium virginicum, Cyperus Schweinitzii, Asclepias amplexicaulis,* and *Ambrosia psilostachya.* This field had been in corn during the previous year.

SUCCESSIONS FROM THE BUNCH-GRASS ASSOCIATION

The bunch-grass association just described belongs typically to the Prairie Province. Of the various associations composing the

vegetation of that province and represented on the sand areas of Illinois, this is ecologically the best fitted to meet the environmental conditions under which it lives. Such associations have been called by Cowles *climax associations* (*1899:* 374, *1901:* 80, 81), a term which is both logical and expressive and which has been generally adopted by American ecologists. Some associations, however, which are relatively stable and consequently more nearly permanent, may under certain conditions give way to others, and to this type may be given the name temporary climax, introduced by Cowles (*1901:* 88) to cover a somewhat different case, but applicable here as well.

Within every vegetation province there is one climax association, which tends to displace every other association with which it comes in contact. For the Prairie Province this seems to be the prairie-grass association (Pound and Clements, *1898:* 389), which is very poorly represented in the areas under discussion. In the Havana area it tends to come in at the bottom of extinct blowouts, which have reached a depth sufficient to expose moist strata of sand (Hart and Gleason, *1907:* 168). In the Hanover area certain tracts of bunch-grass occupying depressions between the dunes are composed of an unusually dense and luxuriant covering of grasses in which *Panicum Scribnerianum* occurs (see description of station 1 of the mixed consocies, p. 66). This species is representative in Nebraska and South Dakota of the prairie-grass association (Pound and Clements, *1898:* 389; *1900:* 348; Harvey, *1908:* 102), and may be considered in our area as a pioneer invader in a prairie-grass succession. The environmental and vegetational differences between the depressions mentioned and the remaining stations of the consocies were not considered sufficient to warrant its separation as an example of the latter association. In other cases where *Panicum Scribnerianum* occurs in the mixed consocies the usual bunch-grasses are so well developed that there is no doubt as to the association concerned.

When associations from two provinces come in contact, local conditions, either climatic or edaphic or both, together with the structure of the associations themselves, decide the supremacy, and one is replaced by the other. In the Illinois sand areas the associations of the Prairie Province are surrounded by those of the Deciduous Forest Province, and the bunch-grass association is under certain conditions succeeded by an oak forest. Certain physical conditions, in this case wind, may also destroy the bunch-grass, and open the way for a series of successions, which generally revert sooner or later to the bunch-grass. The fundamental difference between these two types of succession is apparent. One consists merely of changes within the

Prairie Province; the other is between two provinces, leads to the permanent replacement of the prairie vegetation, and consequently affects the area and the boundaries of both the Prairie and the Deciduous Forest Provinces.

Because of the large area occupied, its resistance to succession by associations of the same province, and its ability to reoccupy the space where it has been destroyed by wind action, the bunch-grass association must be regarded as a temporary climax.

The succession caused by wind will be described first. It begins with the development of the *Panicum pseudopubescens* association, and is followed by a number of associations representing the blowout formation.

THE PANICUM PSEUDOPUBESCENS ASSOCIATION

Notwithstanding the resistance offered by the bunch-grasses to removal of sand by the wind, the exposure of from 20 to 50 per cent. of the surface gives considerable opportunity for aeolian action. Large bunches are not destroyed, and probably not seriously injured, by the removal of sand, but the smaller bunches may be killed. With every subtraction from the vegetative covering more sand is exposed and the effect of the wind correspondingly heightened. One species of bunch-grass, *Panicum pseudopubescens*, can not only endure the removal of sand from beneath it, but seems to thrive better under such conditions than when mixed with larger grasses on more stable sand. As the blowing proceeds, an increasingly larger portion of the surface is occupied by it, until finally it becomes dominant, and the bunch-grass association is thereby converted into the *Panicum pseudopubescens* association. Just where the dividing line between the two should be drawn is questionable. It has been arbitrarily decided that the bunch-grass association must have at least half the surface occupied to be considered typical, and it may also be arbitrarily considered that, in the *Panicum pseudopubescens* association, the characteristic species should constitute at least three fourths of the plant covering. When the vegetation does not comply with these conditions it may be regarded as representing transitional stages of this succession or of other successions.

The best development of this association is in the almost original conditions of the Hanover area, but it also occurs in the Oquawka, Dixon, and Havana areas, presenting the same essential characters in each.

Since the development of the association depends primarily upon

wind action, it does not occupy large continuous stretches, but occurs in isolated tracts of generally small size (Pl. III, Fig. 2). It also shows a very definite space relation to the bunch-grass association and to the blowout associations. The former is normally found at the west and northwest, and the latter are at the east and southeast of the *Panicum pseudopubescens* association. This is caused by the prevailingly west and northwest winter winds, together with the successional relations of the associations.

The circular depressed bunches of the dominant species have already been described under the bunch-grass association. They may grow in almost pure association, as far as other bunch-forming grasses are concerned, or may be somewhat mixed with other species. The additional species, however, are never sufficiently abundant to give the general tone to the association, thereby assuming dominant rank. The bunches are separate or confluent in small irregular patches. The intervening areas of bare sand may be two or three feet (6-10 dm.) across, and are invariably conspicuously depressed between the bunches. The elevated position of the bunches gives them an appearance of prominence and individuality not found in the bunch-grass association. Two other bunch-formers, *Carex umbellata* and *Panicum perlongum*, appear quite frequently. The former produces very dense, flat, circular bunches 1-1.5 feet (3-5 dm.) wide, with narrow, stiff, short, closely aggregated leaves. The bunches are conspicuously elevated, sometimes six inches (1.5 dm.), and the larger ones are invariably dead in the center, thus producing a growth-ring. The outer edge of living plants stands at a conspicuous angle, and the dead center is a few inches above the general level of the sand. The regular hemispherical bunches of *Panicum perlongum* have already been described. In this association they grow somewhat more depressed, approaching in structure those of *Panicum pseudopubescens*. *Carex umbellata* scarcely occurs beyond this association, while *Panicum perlongum* is found in the bunch-grass as well. The amount of ground space occupied by these three plants probably never exceeds 75 per cent., and may be less than 50 per cent.

Several other species of bunch-grasses which occur scattered at wide intervals must be regarded as relics of a former bunch-grass association. They vary in species from station to station, and in number of individuals inversely with the age of the association. They are never abundant, but are frequently very conspicuous because of their larger size or erect habit of growth. The species of this character are as follows:

Andropogon scoparius
Leptoloma cognatum
Panicum virgatum
Koeleria cristata
Boutelona hirsuta
Tridens flavus
Elymus canadensis
Cyperus Schweinitzii
Carex Muhlenbergii

Others of this nature might be expected. Two other grasses, *Paspalum setaceum* and *Sporobolus cryptandrus,* may also occur. They are pioneers, proper to the blowsand and indicative of the probable future succession.

The secondary species, aside from grasses, consist primarily of perennials and interstitials. Correlated with the removal of the sand, the number of species and individuals of the perennials is small, and they are in general to be regarded as relics rather than proper members of the association. The species observed are as follows:

Tradescantia reflexa
Sisyrinchium sp.
Baptisia bracteata
Tephrosia virginiana
Lespedeza capitata
Polygala polygama
Callirhoe triangulata
Viola pedata
Acerates viridiflora
Acerates viridiflora, var. *lanceolata*
Lithospermum Gmelini
Physalis virginiana
Pentstemon hirsutus
Solidago nemoralis
Aster linariifolius
Helianthus scaberrimus

Of these *Lespedeza capitata* is by far the most abundant, with *Helianthus scaberrimus* and *Lithospermum Gmelini* next in importance. Some of the others are represented in single stations, or even by single individuals.

But one instance was observed of the presence of a mat-plant as a relic; *Opuntia Rafinesquii* in the Havana area. This is due to the fact that a bunch-grass association with a good development of mats is far less subject to wind action, and consequently to succession by the *Panicum pseudopubescens* association.

The exclusion of perennials and mats permits a correspondingly larger representation of interstitial species. These come up from seed late in spring and complete their whole cycle of development in the season when the gentler winds and heavier rainfalls keep the sand in a state of relative quiet. The chief species are given in the following list:

Aristida tuberculosa
Festuca octoflora
Cyperus filiculmis
Polygala verticillata
Croton glandulosus, var. *septentrionalis*

Commelina virginica
Rumex Acetosella
Polygonum tenue
Mollugo verticillata
Silene antirrhina
Talinum rugospermum
Lepidium virginicum
Arabis lyrata
Crotonopsis linearis
Oenothera rhombipetala
Monarda punctata
Hedeoma hispida
Linaria canadensis
Erigeron ramosus
Ambrosia psilostachya

Comparing the lists of perennials and interstitials, it will be noted that the latter group is represented by more species, while the number of individuals is vastly greater. The perennials are also infrequent in comparison with the more general distribution of the interstitials. The species in twelve quadrats of approximately four square meters each, in the Hanover area, were listed. The results are shown in the following list, where the numeral indicates the number of quadrats in which the species occurred:

Ambrosia psilostachya (12)
Lepidium virginicum (9)
Lithospermum Gmelini (2)
Oenothera rhombipetala (1)
Croton glandulosus, var. *septentrionalis* (1)
Polygala polygama (1)
Linaria canadensis (10)
Helianthus scaberrimus (4)
Acerates viridiflora, var. *lanceolata* (2)
Solidago nemoralis (1)
Silene antirrhina (1)

The relative frequency of the perennials and interstitials in the list is as 35 to 100. This may be compared with the data given in the description of the bunch-grass association, where in two cases the relative frequencies were as 56 to 100 and as 172 to 100. The interstitial vegetation varies somewhat from place to place, and any species may be locally very abundant. In general, the three leading species in the list are the most important of the group. At any station the species are generally closely similar to those found in the neighboring bunch-grass.

The greatest number of individuals of perennials is found in young associations which have but recently displaced the original bunch-grass, and the number decreases continually with age. The individuals of interstitial species increase in number as the available space becomes larger, but when so much surface is exposed that the blowing of the sand becomes too rapid or continues too long in spring and early summer, the number begins to decrease.

None of the species with conspicuous flowers is abundant enough

to give much color to the association, while the more abundant interstitials have for the most part very small flowers. There is but one season when the association has a well-marked floral aspect. That is during the aestival period when the reddish spikelets of *Panicum pseudopubescens* give a general red tone to the whole. Local displays of color, caused by single plants or groups of *Oenothera rhombipetala*, *Monarda punctata*, or other species, are conspicuous, but not distributed generally over a whole station.

The duration of the association is usually not great. Since both its beginning and end are caused by wind action, its age depends somewhat upon the rate at which sand is removed. If the destruction of vegetation by the wind is aided by heavy pasturing, its duration is still further shortened, and one station in the Havana area contained at the same time relics of the bunch-grass, *Carex Muhlenbergii* and *Leptoloma cognatum*, and pioneers of the blowsand association, *Paspalum setaceum* and *Sporobolus cryptandrus*. Under other circumstances the blowing may cease, and the association then gradually reverts to the original bunch-grass association.

REVERSION TO THE BUNCH-GRASS ASSOCIATION

The dominant or climax nature of the bunch-grass association has already been mentioned. Whenever those physical conditions which are concerned in producing the *Panicum pseudopubescens* association become inoperative or ineffective, a reversion to the original vegetation begins. This may take place with considerable rapidity, because of the usual proximity of the two associations and the consequent readiness with which migration may take place. Reversion begins not only near the margin of the association, but in the center as well, if that part has ceased blowing. This succession has been observed only in the Hanover area, but undoubtedly occurs at any other place where both associations are present and the environmental conditions are suitable.

The pioneer invader in the Hanover area is *Selaginella rupestris*. Its habit of growth in circular patches allows a comparative estimate of the age of different stages in the succession. Some stations of the *Panicum pseudopubescens* association were observed which were apparently normal except for a few small, regularly circular mats of *Selaginella* near the margin. The number, size, and regularity of the mats all indicate an early stage in the reversion. Later it becomes so abundant that it may form a solid mat on the ground, in which the rings are of large size and overlap each other. Ac-

companying it is an increased development of *Boutcloua hirsuta,* which, as already noted, may almost be regarded as a mat. Until the mats become continuous there is an excessive growth of the usual interstitial plants. *Aristida tuberculosa, Ambrosia psilostachya,* and *Monarda punctata* are especially abundant, and the others of less frequency are *Talinum rugospermum, Specularia perfoliata, Erigeron ramosus,* and *Arabis lyrata.* The latter species frequently grows by the hundred upon the mats of *Selaginella. Opuntia Rafinesquii* also occurs rarely, and the only known Illinois station for *Opuntia fragilis* is in one of these reversional stages and the adjoining bunch-grass association. The perennials probably include both pioneers and relics, but they can not be distinguished in the field. Those observed are *Aster sericeus, Aster linariifolius, Pentstemon hirsutus, Callirhoe triangulata,* and *Lithospermum Gmelini.* Beside the normal bunch-grasses, scattered bunches of other species occur, which may be either relics or pioneers.

As the *Selaginella* mats grow older they become dark and charcoal-like in appearance and are frequently occupied by crusts of *Cladonia.* At a later stage small mats of *Antennaria* come in.

The order of entrance of the bunch-grasses was not observed, but depends largely upon the nature of the neighboring areas of the bunch-grass association. At the border of some of these reversional stages, portions of extremely large mats of *Selaginella* were found in the bunch-grass, indicating the invasion of the grasses from the margin toward the center. The dense mats of *Selaginella* probably serve to check their rapid development.

The Blowout Formation

Of all the features of the action of the wind upon sand, the saucer-shaped or bowl-shaped excavations known as blowouts are the most peculiar (Pl. VII, Fig. 2; Pl. VIII, Fig. 1). Blowouts probably occur in every large unforested sand region. They reach a large size and a considerable depth, and are frequently a prominent feature of the landscape. The physical conditions and the movement of the sand within them have apparently not been fully described, and the vegetation of American blowouts is still very imperfectly known.

Cowles (*1899:* 195-197) mentioned the blowouts or "wind-sweeps" of the south shore of Lake Michigan, but did not describe the vegetation in detail. As usual, they stand in a direction parallel to the wind, and may reach down almost to the water-level. One of them, at Dune Park, Indiana, has steep sides from 30 to 60 feet

(10-20 m.) high, making it much deeper than any in the inland dunes of Illinois. Developing in the midst of moving sand, they may have a different structure and different plant associations from those of the inland regions.

Rydberg (*1895:* 135) described blowouts in the sand-hill region of Nebraska which were 100 yards (100 m.) in diameter and from 50 to 60 feet (15-20 m.) deep. He mentioned how sand slides down from the sides into the basin, but did not describe similar behavior of the vegetation. Certain grasses, as *Calamovilfa longifolia, Redfieldia flexuosa, Eragrostis trichodes,* and *Muhlenbergia tenuis,* colonize in the basin and take part in the stabilization of the blowout. Of these four grasses, *Calamovilfa* and *Eragrostis* live also in the Illinois sand region, but not in blowouts. Rydberg's work was mainly taxonomic in its aims, and the ecological notes which he gives are merely incidental.

Pound and Clements (*1900:* 365-368) later studied the same region from an ecological standpoint, and have given the best description of blowouts and their vegetation. *Redfieldia flexuosa* and *Muhlenbergia pungens* are "habitually and almost exclusively blowout inhabitants." These two grasses are pioneers in binding the sand and creating conditions suitable for other plants. Stabilization apparently begins at the bottom, and ultimately the whole blowout is reoccupied by the bunch-grass vegetation. The description does not give an idea of the structure or vegetation of the other parts of the blowout, which are probably the same in Nebraska as in Illinois. In an earlier paper (*1898:* 392) Pound and Clements described the Nebraska blowouts in a short paragraph, and indicated that the life of a blowout from formation to stabilization may be about ten years. In both papers the "sand-draw" formation is also described (*1898:* 392; *1900:* 368-370). In neither case does the description give a clear idea of the vegetation or the environmental conditions, but it seems probable that the vegetation is somewhat similar to the blow-sand association of this paper. No similar habitat occurs in Illinois

Jennings (*1908:* 324-326) has described blowouts on Cedar Point, near the western end of Lake Erie, which extend down to a former surface level, or fossil beach. On them there is developed sometimes a heath vegetation of *Arctostaphylos Uva-ursi* and *Juniperus,* and sometimes an association characterized by *Artemisia caudata* and *Panicum virgatum.* The complex nature of the blowouts was recognized but the successions which led to their stabilization were not worked out. In a later paper on the vegetation of Presque Isle (*1909:* 313-318) Jennings regards his *Artemisia-Pani-*

cum association as equivalent in habitat to the Illinois blowouts. There are some species in common, but in the opinion of the present writer there is not sufficient resemblance in habitat or flora between the two to justify their classification in the same ecological group.

The only ecological discussion of the inland region of Illinois is by Gleason (Hart and Gleason, *1907:* 162-167, 169-171). The origin, growth, and stabilization of the blowouts of the Havana area were discussed and the typical plants were listed. The different physiographic parts of the blowouts, and their four plant associations and the various successions between them were not recognized.

In the normal development of a blowout, it probably always follows the *Panicum pseudopubescens* association, and consequently appears at the eastern side or in the center of that association. When its development begins in the bunch-grass association, without the intervention of an intermediate society, it is probable that its inception is due to some extraordinary local cause. The stamping of grazing cattle has been suggested as a possible cause, and in one case a blowout started from a hole excavated in removing sand for building purposes.

If a single blowout can increase in size without coming in contact with any others, it shows certain definite physiographic features which appear to be constant. More often, however, several blowouts originate near each other, and, becoming confluent with growth, they form a complex waste of sand (Pl. IV, Fig. 2) which baffles physiographic analysis and sometimes causes the greatest difficulty in classifying the meager vegetation. A complete typical blowout (Pl. IV, Fig. 1)contains four parts, extending from west to east in the direction of the prevailing winds. As a matter of fact the direction of the axis of the blowouts may vary from north-south through west-east to south-north. In the following discussion the direction is always spoken of as west-east, for the sake of brevity. At the western end there is a downward slope from the general level, here termed the windward slope. From it sand is being removed by the wind toward the east, and is also settling down by gravity toward the bottom of the slope. The windward slope generally occupies a more or less crescent-shaped area extending partly around the north and south sides of the blowout. The deepest portion is termed the basin, and from it sand is being rapidly carried away by the wind. Some is also being deposited by wind and gravity from the windward slope, but the resultant is in favor of the general removal of sand. A crescent-shaped sloping area toward the eastern end of the blowout is termed the lee slope. There the rates of erosion and deposition are about

equal; the sand is constantly changing although its level varies but little. Finally an outer crescent, called the deposits (Pl. V), surrounds the lee slope and is somewhat higher than the general level. As its name indicates, it is composed of sand removed from the other three parts and carried up by the wind. A longitudinal section through a typical blowout is shown in Figure 4. The basin shows a constant

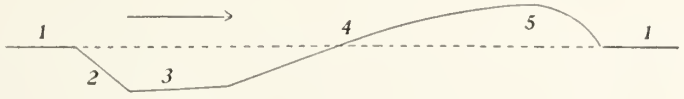

Fig. 4. Diagrammatic longitudinal section through a typical blowout. *1*, original level of sand; *2*, windward slope; *3*, basin; *4*, lee slope; *5*, deposits.

tendency to increase in size or in depth. If this tendency is most pronounced toward the rear, i.e., the west, it is shown by a steep windward slope; if most pronounced toward the front, or east, by gentle windward and steep lee slopes. If all the sand removed is poured out in one direction, the sides become steep and settle by gravity toward the basin. They may be regarded as a continuation of the windward slope and are occupied by the usual vegetation. On the other hand, if the sand is carried out toward the north and south as well as toward the east, the windward slope is small, and the lee slope and deposits extend around three sides of the blowout. Between the two extremes there is every imaginable gradation. A blowout of this simple type is occupied by four plant associations which are usually easily recognizable and which are correlated with the four physiographic divisions.

The maximum observed length of a simple blowout, but without all four parts present, is in this region about 200 yards (200 m.). As their size increases the windward slope may disappear, either by a reduction in its gradient or by stabilization. The continuous crescent of deposits may be broken up into several detached segments, separated by patches of sand corresponding to a lee slope or by promontories covered by bunch-grass and with vertical walls. The slope below these steep-sided mounds usually functions as a windward slope, and is occupied by the characteristic vegetation, even though it is at the eastern end of the blowout. There is also a general progressive movement of the blowout from west to east, so that the stabilized remains of an old windward slope may be found behind the present active one.

Blowouts of this simple type are not common; in fact only one

of large size was observed in which all four parts were present without any apparent modification. Deviations from the normal may usually be referred to three general causes: (1) the blowout is young and not all the parts are developed (Pl. VI, Fig. 1; Pl. VII, Fig. 1); (2) the blowout is old or has ceased its development and part or all of it has become stabilized by the action of plants (Pl. XI, Fig. 2); or (3) two or more blowouts have grown together or smaller secondary blowouts have begun within them, interfering with the regular arrangement of the physiographic features and plant associations (Pl. IV, Fig. 2). Any two, or all three, of these may act together. Observation shows that stabilization may begin in any part of the blowout, whether it is young and small or large and old. When two or more blowouts grow together, the most usual disturbance in their regularity is the combination of the two deposits or the filling of the basin of one by the deposits of the other. The larger the space occupied by the blowout complex, the smaller is the probability of stabilization and the greater the amount of loose sand exposed to the wind. The complex may then occupy several acres of ground and be an actual menace to agriculture in the vicinity (Pl. X, Fig. 1). When in this condition it is locally known as "wild sand." The most notable complex in this respect is the waste known as the Devil's Neck, in the Havana area north of Topeka, where more than forty acres of land is covered by shifting dunes, which have a maximum height of probably 50 feet (15 m.). Blowouts may sometimes develop on the west side of a hill, in which case the windward slope, if any, is composed of one or two lateral slopes on the north and south sides. The basin is relatively high and the bunch-grasses at the windward end are removed by wind alone and not by gravity. Blowouts may also develop on the east side of a hill (Pl. VII, Fig. 1), resulting in a strongly developed windward slope, and in a lee slope and deposit which may be actually lower than the basin.

Attention must be called to the fact that the general effect of the wind is to reduce the elevations and fill up the depressions of the surface. The dunes themselves are initiated and perpetuated by the growth of plants upon their summits. This has been well described by Cowles in his report on the dunes of Lake Michigan (*1899:* 175-190.) Even the migrating or wandering dunes, although carried forward by the wind, leave a trail of sand behind, which would soon exhaust them if continued very far. In a somewhat similar way there is a limit to the size and depth of the blowouts. At the maximum depth the wind is no longer able to lift sand up the lee slope from the basin. If too wide,

the currents of the wind are changed and the bottom of the blowout ceases to be eroded. The basin is thus converted into an extension of the lee slope, where the sand is merely in motion, without an essential change in level. Very little information is available concerning the rate of movement of the sand. That the motion is continuous through the summer is shown by a rough experiment in the Hanover area. A hole about eight inches (2 dm.) deep was dug June 2, 1908, on a flat expanse of sand, with no vegetation except a few plants of *Hudsonia*. On June 13 it was found filled to a depth of two inches (5 cm.). This does not indicate erosion or deposition, but merely the amount of sand which traveled across the area in the given time and was caught in the hole.

In spite of the physiographic diversity, the vegetation, if any, can be referred to four different associations. One of these, which from its position may be called the windward slope association, is primarily relict in its nature, being derived from the bunch-grass or the *Panicum pseudopubescens* association. The basin association consists of a very sparse growth of perennials, analogous to those described by Pound and Clements (*1898:* 392; *1900:* 365) in similar situations in Nebraska. The lee slope is occupied by the blowsand association, limited in duration and consisting almost entirely of annuals. Lastly, the deposit association is composed chiefly of sand-binding perennials, which serve to build up the deposits into dunes. Each of these associations is well correlated with the dynamic conditions of its environment; so well correlated in fact that the vegetation is one of the chief means of recognizing the nature or rate of movement of the sand. When the different physiographic parts are obscured or obliterated in a complex of blowsand, the vegetation is still correlated with the dynamic conditions, and the nature of the movement of sand may be compared with accuracy to the appropriate portion of a normal blowout where the same vegetation is developed. Care must of course be exercised to avoid confusing relics with the typical plants of the station.

The specific composition of each of these associations varies greatly from area to area and from blowout to blowout. The variation is frequently perplexing, and becomes especially so when the number of species is small and the individual plants few or scattered. Relics of a preceding vegetation are also frequently found and add considerably to the difficulty of distinguishing the associations.

The development of a blowout in the prairie is first evidenced by an exposed area of bare sand surrounded by the *Panicum pseudopubescens* association. The young blowout may in fact be regarded

as a mere expansion of the spaces between the bunches. The sand thus exposed is but slightly concave, indicating that wind erosion has only begun. The small quantity of sand removed is piled up in a scarcely perceptible heap along the lee side of the blowout. There is then at the outset a differentiation of two of the physiographic parts, the basin and the deposits, and each of these is soon occupied by its characteristic association. The windward slope and the lee slope may not appear at first, but may be consequent upon the greater development of the excavation.

THE BASIN ASSOCIATION

The basin has always the most meager vegetation of the blowout, and in the first stages is either absolutely bare or occupied by one or two perennials left as relics from the *Panicum pseudopubescens* association. The annual interstitial plants, so abundant in that association, do not grow here because of the removal of sand, which prevents the proper planting of their seeds, as will be shown later. As the blowout deepens and widens, a few hardy deep-rooted perennials appear in the bottom, and these constitute the basin association proper. Most notable among the few species is *Acerates viridiflora* and more especially its varieties *lanceolata* (Pl. VI, Fig. 2) and *linearis*. The varieties reach here their largest size and best development. The roots go down to a very great depth; the stems are one to five in number and lie prostrate on the sand. *Acerates viridiflora,* var. *lanceolata* blooms and produces fruit in this precarious situation; *A. viridiflora,* var. *linearis* has not been seen in fruit or flower, is always smaller in size, and may possibly be a juvenile form of the other variety. These two varieties are more widely distributed and more frequent in the basins than in any other habitat. Many blowouts are entirely bare in the basin except for a single individual of the variety *lanceolata*. The plants are never numerous, but are conspicuous because of the absence of other species. They are known to occur in the Hanover, Oquawka, and Havana areas, and doubtless occur in other regions where blowouts are developed. They also grow in the bunch-grass and *Panicum pseudopubescens* associations, but are never common. It may be that in some blowouts they are merely relics, but their number and frequency in that situation are incompatible with their distribution outside. Again, they have not been seen on the windward slope, where relics might be expected. Also, the only plant in a small secondary blowout, newly excavated on the deposits of an older one, was a single plant, exactly

in the middle, of the variety *lanceolata*. Considering all lines of evidence, it seems conclusive that these two varieties find their optimum habitat in the basins, colonize in the blowouts after the basin is formed, and occupy a place similar to that of the grass *Redfieldia* in the blowouts of Nebraska. The other species represented in the blowouts are *Lithospermum Gmelini*, *Euphorbia corollata*, and *Lespedeza capitata*. Each of these has deep roots, but they can not live in the more active blowouts, which are either bare or with *Acerates* alone. Rarely a few annuals, of species occurring also on the lee slope, are found with *Acerates*, but it seems probable that their occurrence indicates at least a partial or temporary cessation of wind erosion. If this is the case, they should be regarded as a mere extension of the blowsand association, in which the *Acerates* is persisting as a relic. The perennial *Lespedeza capitata* is also good evidence of the same condition, since, as will be shown later, it is one of the most abundant pioneer species in the stabilization of this part of a blowout.

THE WINDWARD SLOPE ASSOCIATION

As the erosion of the blowout proceeds, the windward slope is formed, as already described. From this, sand is being removed by the wind and is also settling down by gravity. There is little chance for seed burial, because the same wind that carries out sand will also blow away the seeds, and as a consequence the annual plants are absent. But the action of gravity, which brings down sand from above, may also bring down plants. The principal vegetation, therefore, is composed of perennials or grasses of the *Panicum pseudopubescens* association which are undermined and gradually slide down the slope into the basin. The most frequent species is *Panicum pseudopubescens* itself, which seems admirably adapted to live in this shifting substratum. Its usual associate, *Carex umbellata*, also has the same property. These two species seem able to live on this slope under almost any condition of angle or rate of erosion. Scattered bunches may be found on the steep slope below vertical walls of sand capped with the same species. The wall is held vertical by the roots of the grass, until finally a portion of it topples over. If the grasses happen to fall right side up they continue their growth and eventually land at the foot of the hill. Many, if not all, of the remaining grasses of the same association appear on the gentler windward slopes, where the erosion takes place more slowly. The grasses observed are *Leptoloma cognatum*, *Carex Muhlenbergii*, *Andropogon scoparius*, *Bouteloua hirsuta*, and *Panicum virgatum*. *Lespedeza*

capitata is the most abundant perennial. In one blowout the original bunch-grass association was being undermined: *Viola pedata* and whole mats of *Selaginella rupestris* were not only sliding down the slope, but persisting at the bottom. *Viola pedata* holds a small dune at its base until the erosion gets below the level of its roots, when the whole miniature dune slides down with the plant.

At the bottom of the slope the plants are usually undermined completely and their dead remains are blown away. But if the erosion of the basin is slow they may persist. One blowout (Pl. XI, Fig. 2) in the Oquawka area showed a semicircle of established bunches of *Panicum pseudopubescens* and *Leptoloma cognatum* at the base of the slope, and in their shelter numerous annuals were beginning to colonize.

The vegetation of the windward slope is very open, with at least 90 per cent. of the sand exposed. The individual bunches stand at a much greater interval than in the association above the slope, because only a portion of them survive and the gradual settling tends to separate the remainder.

THE BLOWSAND ASSOCIATION

The lee slope of the blowout, unless the rate of movement is unusually rapid, is occupied by a variable group of annual plants, most of which live also as interstitials in the bunch-grass and *Panicum pseudopubescens* associations. As has been mentioned, the lee slope is an area characterized neither by erosion nor deposition, but by the mere movement of sand. Most of this movement affects only the surface, or extends to but a slight depth. Every autumn and winter countless seeds are blown across the blowouts. There is virtually no chance of their being covered to the requisite depth on the windward slope or in the basin, because there erosion is active. Consequently both of these associations are almost entirely without annuals. But on the lee slope, where the upper layers of sand are almost always drifting, there is a good chance that some of the seeds will be left covered to a depth of an inch (2.5 cm.) or more. This seems to be the minimum depth at which germination takes place, and marks the upper limit of moist sand during the rainy season in June. It is quite probable that this minimum fluctuates with the amount of rainfall, and may be much deeper in drier years (cf. Britton, *1903:* 577).

In late spring and early summer the seedlings appear, and the frequent presence of thousands of dead stems of *Aristida tuberculosa*

indicates that the level, in some places at least, has changed but little since the preceding autumn. Elsewhere seedlings appear on ground without dead stems, indicating that conditions were probably unfavorable for seed planting during the previous year. It may be assumed also that certain tracts covered with plants during one year may be bare the next, because of some slight change in the velocity or direction of the sand movement. So the position and extent of the blowsand association vary from year to year, now extending lower and possibly surrounding some relics of the basin association, now retreating toward the summit of the slope, but always appearing where the movement of the sand tends to bury the seeds to a small, but sufficient depth.

The species of the association vary in their ability to extend out upon the sand. *Aristida tuberculosa* is always the pioneer, and the margin of the association frequently consists of that species alone. This is probably due to the awned grains, which may be able to bury themselves to some slight depth. The grains of *Stipa spartea*, with much longer and stiffer bent awns, are known to bury themselves to a depth of about two inches (5 cm.). Places most densely covered with *Aristida* usually have several other species as well, and their contour generally shows that upon them small deposits, generally less than an inch (2.5 cm.) deep, have taken place. Other conditions being eliminated, small seeds are more apt to be buried than large ones, and it is at once noticeable that the individuals of species with small seeds are vastly more numerous than those with larger ones, as *Cassia Chamaechrista*.

The necessity of seed burial is strikingly illustrated by seedlings coming up in rows over wagon tracks. This has already been mentioned for *Cassia Chamaechrista* (Hart and Gleason, *1907:* 165) and, in a short note (Amer. Botanist *7:* 91), for *Diodia teres*. A blowout in the Hanover area illustrates the effect especially well (Pl. VIII, Fig. 2). At the very edge of the lee slope, where erosion has probably exceeded deposition, there are several curving rows of *Diodia teres*, marking the tracks of a wagon which had been driven in a curve across the sand. To be effective this artificial planting must be deep enough to prevent the seeds from being uncovered by any subsequent erosion.

The species comprising the association, arranged approximately in the order of their abundance, are as follows:

Aristida tuberculosa
Paspalum setaceum
Diodia teres
Commelina virginica
Cenchrus caroliniamus
Ambrosia psilostachya

Cassia Chamaecrista
Sporobolus cryptandrus
Oenothera rhombipetala
Croton glandulosus,
var. *septentrionalis*
Euphorbia Geyeri
Froelichia floridana
Tephrosia virginiana
Cyperus filiculmis
Cycloloma atriplicifolium
Festuca octoflora
Polanisia graveolens
Helianthus lenticularis
Hedeoma hispida
Euphorbia corollata
Mollugo verticillata
Polygonella articulata
Crotonopsis linearis
Linaria canadensis
Cristatella Jamesii
Monarda punctata
Lepidium virginicum
Lespedeza capitata
Strophostyles helvola
Apocynum cannabinum,
var. *hypericifolium*
Scutellaria parvula

The majority of these 31 species are annuals, and appear also as interstitials in the bunch-grass and *Panicum pseudopubescens* associations. One, *Apocynum cannabinum,* var. *hypericifolium,* is a perennial, but behaves as an interstitial in this habitat. Its occurrence was noted but once. The three true perennials, *Euphorbia corollata, Lespedeza capitata,* and *Tephrosia virginiana,* and the one bunch-grass, *Sporobolus cryptandrus,* are all more numerous on the deposits or in other associations, and their presence here is either casual or else indicative of a succession by the deposit association.

But one species, *Aristida tuberculosa,* is equally common over the four areas studied. Scarcely a blowout was observed which did not have hundreds of plants of this slender grass growing on the lee slope. The other leading species are more local in their distribution. *Diodia teres* is particularly characteristic of the Hanover area, is also common, but local, in the Havana area, but was not observed in the other two areas. The Oquawka blowouts are marked especially by *Commelina virginica* and *Paspalum setaceum,* while *Cenchrus carolinianus* is most abundant in the Havana area.

Excluding the Dixon area, in which there is comparatively little blowing sand, from 17 to 22 of the 31 species occur in each area. Within each area the flora varies from one blowout to another, and a comparatively small portion of the flora appears in any one. Notwithstanding this great local variation between stations, there is no evidence that more than one association exists. The different combinations of species represent merely alternations in the structure of the association, which are not definite enough to demand classification or description as separate consocies.

An interesting phenomenon caused by the dead stems of *Aristida tuberculosa* is frequently observed in the spring and early summer. The dead culms of the preceding year lie flat on the sand but remain firmly attached at the base. When blown by the wind they swing around in arcs of a circle and the tips scratch concentric curves in the sand. The maximum diameter of these wind circles is about three feet (8 dm.), and the average arc about 60 degrees, although some complete circles were observed.

THE DEPOSIT ASSOCIATION

The chief difference in physical environment between the lee slope and the deposits is the nature of the movement of the sand. On the deposits sand is being added by the wind more rapidly than it is being moved away, so that there is a gradual increase in height. This soon leads to the development of a ridge, its size depending naturally on the size of the basin which furnishes the sand. When sand is piled up by wind alone, unimpeded by obstacles of any sort, it is distributed rather uniformly over a considerable area. The resulting dune has a very gentle windward slope and a slightly steeper face. According to Cowles these slopes are about 5 degrees and 30 degrees respectively (*1899:* 191). Sand can not accumulate to a great depth because of the full exposure to the wind, and the dune is sometimes so flat that it almost escapes attention. The blowouts in the Oquawka area are particularly notable for their broad, flat deposits, which are usually not more than three or four feet (1 m.) above the general level. Their vegetation differs but little from that of the lee slopes of the blowout.

For building up the steeper dunes, so characteristic of the blowouts in the Hanover area, the wind alone is not sufficient. There must be an obstacle of some sort which will cause the wind to drop much of its load of sand at one spot, and which will also prevent its removal by other winds from the same or different directions. This obstacle must grow up with the dune, otherwise it would eventually be covered and its efficiency destroyed, and it must last through the winter, when the wind is strongest. All of these conditions are met only by plants, a few species of which become, because of their growth habits, the chief dune-builders of the region. Cowles has shown very clearly the necessary characteristics for a good dune-forming plant (*1899:* 175-190). They are (1) a perennial life, (2) the ability to spread radially by rootstocks (with certain exceptions), (3) the power of growing out into the light when buried

by sand, (4) the ability to adapt the root to a stem environment or the stem to a root environment, depending upon burial by sand or exposure by its removal, and (5) a good set of xerophytic structures, which enable the plant to withstand the extreme conditions of its environment. To these might be added a sixth requisite, the persistence of the subaerial parts during the winter. In every dune region there are some plants which fulfil all or some of these requirements, and which are responsible for the construction of the local dunes. In Illinois the principal ones are *Rhus canadensis,* var. *illinoensis, Ceanothus ovatus, Panicum virgatum,* and *Tephrosia virginiana.* These are discussed in the order of their effectiveness.

Tephrosia virginiana (Pl. IX, Fig. 1) is a perennial herb with very long, slender, tough roots. Several stems, each 1-1.5 feet (3-4 dm.) high, arise from a common base and are densely covered by leaves. These serve to catch the sand and hold it during the summer, but they die in autumn and the dead stems are soon removed by the winter storms. The sand is then held by the subterranean root system only. *Tephrosia* endures covering by sand if it is not to too great a depth, at least not exceeding half the height of the stems. It does not possess the power of unlimited growth during the season, and is consequently not able to keep above the sand indefinitely. Neither is it a very efficient sand-binder, and it dies if the crown and a few inches of the roots are exposed (Pl. IX, Fig. 2). Such cases are seldom seen, because the dead remains are soon blown away. From both of these reasons it is clear that *Tephrosia* is not a very efficient dune-former, and this is fully substantiated by field observation. *Tephrosia* dunes are low and gently sloping (Pl. VII, Fig. 2), and are found mainly on blowouts where the rate of sand movement is apparently very slow. This, of course, does not prohibit the plant from growing on larger dunes in company with other species. It is always associated with *Aristida tuberculosa.*

Panicum virgatum is by all odds the most abundant dune-former in the Hanover area (Pl. IV, Fig. 2). While it does occur in the bunch-grass association, it is much more abundant on the deposits, and in the area mentioned even the smallest and youngest blowouts are sometimes marked by a conspicuous growth of the plant on their newly formed deposits (Pl. VI, Fig. 1; Pl. VII, Fig. 1). In the Havana and Oquawka areas it is infrequent, and the dunes are usually formed and held by some other species. Like *Tephrosia,* it has a large number of very deep tough roots which help bind the sand, and it also spreads slowly by rhizomes. The subaerial parts have the typical bunch-grass structure, and the dense basal leaves act

efficiently in catching and holding the sand during the summer. After the death of the leaves and culms in the autumn, they still persist, and continue to build up the dune during the winter. These dead bunches are frequently partly covered, but the new growth of the succeeding spring comes up through the sand, and bunches entirely destroyed by burial were not observed. The species is accordingly a very efficient dune-former, and builds up steep dunes from two to ten feet (1-3 m.) high. The infrequency of the plant in situations from which sand is being removed gives no opportunity to estimate its ability to withstand uncovering. In a few cases relic bunches have been seen on windward slopes, but it is probably not well adapted to undermining.

Rhus canadensis, var. *illinoensis*, while not so abundant as *Panicum virgatum,* is the most effective dune-former in our inland dunes. It is characteristically a species of the open bunch-grass association (Pl. VII, Fig. 1), where it produces dense rounded thickets up to a yard (1 m.) in height and frequently several yards across. These thickets are so dense that at a little distance they appear as a solid mass of foliage. Within there is a tangle of stems, with the leaves mostly near the ends. The roots are long, and penetrate very deeply into the soil. Fruit is produced abundantly and is probably scattered widely by birds, yet comparatively few young plants are seen and none at all have been seen on the deposits of the blowouts. Its presence there is probably in most cases due to persistence from the bunch-grass which preceded the blowout. It may occur, therefore, at either side or at the deposit end. The number of blowouts where it so occurs depends upon its frequency in the adjoining bunch-grass. It has not been observed in the *Panicum pseudopubescens* association or on the windward slopes of the blowouts. The efficiency of the plant in building up dunes is due to its habit of growth in dense compact masses and to its ability to withstand burial by sand. The blowing sand is caught and held by the dense thickets, and accumulates in a rounded heap conforming to the shape of the thicket. The accumulation continues until the sand reaches within six or eight inches (1-2 dm.) of the top of the thicket. There is little difference in the outward appearance of such a partly buried thicket, although the leafy twigs protrude but a few inches above the sand. When the leaves fall in autumn they also tend to accumulate between the twigs and thus protect the sand from erosion during the winter. The sumach is not injured by this partial burial, but in each successive season grows farther upward and outward, maintaining its position above the sand and causing the rapid growth of the dune.

As the thicket becomes larger, portions of it may die away and leave unprotected areas between smaller thickets. These bare spots are usually one or two feet (3-6 dm.) below the general level of the dune, indicating the erosion of the sand after the death of the sumach. The steepest and highest dunes are invariably held by the sumach. The highest ridges along the Mississippi river, which will be described later, are usually crowned at their very summits by scattered patches of sumach, whose large size and irregular outlines bear witness to their great age.

Ceanothus ovatus behaves in a way similar to *Rhus*, but is much rarer. It is more susceptible to injury by burial and does not possess so great a capacity for unlimited growth above the accumulating sand. *Ceanothus* dunes have been observed only along the Mississippi river in the Hanover area.

Besides these plants which are of chief importance, a few other perennials or grasses may locally aid in building up dunes. They are, however, generally temporary in their nature and persist only during the summer when the plants are growing. Their size depends upon the habit of the plant, but seldom exceeds a foot in height. The larger dunes of this type are formed by *Euphorbia corollata*, *Stipa spartea*, *Sporobolus cryptandrus*, and *Paspalum setaceum*. Even annuals, if growing in close patches, may accumulate an inch or so of sand around them. *Euphorbia Geyeri* and *Mollugo verticillata*, the two common prostrate species of the deposits, do not accumulate sand, but their flat close mats prevent erosion if it is not too rapid. They are sometimes seen growing on plateaus a half-inch (1-2 cm.) in height, and corresponding with the shape and size of the plant. *Mollugo* reaches its largest size on the deposits, forming mats sometimes two feet (6 dm.) across.

Two general types of deposits may be distinguished: those with and those without effective sand-binders. Examples of the latter class are broad and low with gentle slopes, and scarcely differ in vegetation from the neighboring blowsand association, of which they may be considered an extension. When the blowout is young and small the annual increment of sand is but a few inches thick and affords optimum conditions for the burial of seeds of the annuals. The young deposits are accordingly covered with a dense growth of these plants, and under such circumstances may be regarded, as far as the vegetation is concerned, as extensions of the lee slope. If efficient sand-binders do not appear on the deposits with the subsequent growth of the blowout, the vegetation remains essentially the same, except for the addition of various species of perennials. The most

abundant grasses, *Cenchrus carolinianus* and *Paspalum setaceum,* are not injured by burial to a slight depth, but are easily undermined. They find their optimum conditions on deposits of this type, where their fruits are easily buried and where the annual deposit of sand is not sufficient to injure them. If the deposition becomes too rapid and the fruits are buried too deeply, the sand remains entirely bare (Pl. V). The best observed example of this condition is a large dune just south of Keithsburg, in the Oquawka area (Pl. X, Fig. 1). The top of the dune is here entirely bare. At its base along the lee side is a zone of sparse vegetation consisting of *Helianthus lenticularis, Euphorbia corollata, Cenchrus carolinianus, Cycloloma atriplicifolium* and *Lespedeza capitata.* A line of dead plants of *Helianthus* shows that the annual forward movement of sand is about 15 feet (5 m.).

None of the four most efficient sand-binders is abundant in the Oquawka area, either in the bunch-grass or on the deposits. The blowouts there are mainly broad and shallow, with similarly broad flattened deposits, spreading out fanwise over a large area. They are occupied especially by *Cenchrus carolinianus* and *Paspalum setaceum,* with most of the species of the blowsand association. With these are a few additional species, such as *Sporobolus cryptandrus, Leptoloma cognatum, Panicum pseudopubescens, Bouteloua hirsuta,* and *Lespedeza capitata.* These five species do not occur on the regular lee slopes, and represent the deposit association in the narrower sense. The Havana dunes resemble those of the Oquawka area and have in general the same vegetation. *Paspalum setaceum, Cenchrus carolinianus,* and *Sporobolus cryptandrus* are the usual species. Deposits of this type occur rarely in the Hanover area also, and then generally in connection with secondary blowouts which have developed on parts of other larger ones. They are especially characterized by the abundance of *Diodia teres.*

The second type of deposit is marked by the presence of effective sand-binders, and is best developed in the Hanover area. Usually *Panicum virgatum* or *Tephrosia virginiana* appears immediately on the youngest deposits and begins at once the building of the dune. They may appear at a later stage, but in either case the result is the same. Dunes may be held by *Panicum* or *Tephrosia* or by both together. They seldom appear in association with *Rhus,* probably because the rate of increment of a *Rhus* dune is too rapid to permit their growth there. Associated with them are a large number of annuals, such as occur also on the lee slopes. They are most numerous on the *Tephrosia* dunes, which are of relatively slow growth, and least numerous on the rapidly growing *Rhus* dunes. If the

dune is held by *Panicum virgatum,* it is usually distributed uniformly around the deposits, and the dune is approximately uniform in height. The bunches of grass are seldom more than a yard or two apart and most of the intervening space is occupied by annuals. *Stipa spartea, Andropogon furcatus,* and *Carex Muhlenbergii* are sometimes associated with *Panicum* and are probably relics. *Carex umbellata, Panicum pseudopubescens, Koeleria cristata,* and *Viola pedata* are less frequent and are undoubtedly relics. Because of the relic nature of the sumach on the deposits, a dune seldom has more than one thicket of it. At that place the dune rises much above the general level and has steep slopes occupied by relatively few other plants. At a little distance from the sumach thicket the bunches of *Panicum* and *Tephrosia* appear. On such blowouts the deposits frequently become irregular or one-sided, or the direction of deposition may be changed, because of the greater efficiency of the sumach as a sand-binder.

SUCCESSIONS BETWEEN THE ASSOCIATIONS OF THE BLOWOUT FORMATION

As the *Panicum pseudopubescens* association becomes more open and more bare sand is exposed in the formation of a young blowout, it is difficult to decide just where the dividing line between the two types of associations should be drawn. For convenience it may be considered that a blowout begins with the first appearance of areas of deposition and erosion, that is, with the differentiation of basin and deposit. These two physiographic structures are very soon occupied by their usual vegetation. The windward slope and its attendant plant association appear as soon as the increasing size and depth of the basin begin to disturb the bunches of *Panicum pseudopubescens* in the rear. Between the basin and the deposits there must be at least a small space where the movement of sand is about neutral, and this represents an incipient lee slope. The typical vegetation, however, does not appear during the earliest stages of the blowout. The four associations, therefore, appear in the following order: (1) the basin and deposit associations, (2) the windward slope association, (3) the blowsand association.

These four physiographic parts constitute a definite series as to structure and development, but their vegetation does not fall into a regular successional series. That is, an area now occupied by the windward slope association may not, and probably will not, be occupied in turn by the basin, the blowsand, and the deposit associations. The successions are, instead, very complicated and irregular.

The successional relation between the *Panicum pseudopubescens* and the windward slope associations is self-evident, since there is an actual transfer of individuals from the former to the latter. The basin is developed directly within the *Panicum pseudopubescens* association by a mere change in the nature of the sand movement, and also represents a direct succession. Because of the environmental conditions there are seldom any relics which survive. The succession represents a case where the preceding vegetation is entirely destroyed before the next stage appears. The deposit association also succeeds the *Panicum pseudopubescens* association directly and relics frequently occur. On the lee slope the movement of the sand is similar to that going on in the intervals between the bunch-grasses, so that the blowsand may be regarded as another direct succession. All four associations of a typical blowout, therefore, may and do arise simultaneously and independently.

The general appearance of a typical young blowout is shown in Plate VI, Fig. 1. The total width of the blowout from west (left) to east (right) is about 20 feet (6 m.). At the left is the edge of the *Panicum pseudopubescens* association, with many relic bunches of *Andropogon scoparius* and in the extreme left foreground a bunch of *Carex Muhlenbergii*. From this will develop the windward slope association. Along the right is a conspicuous zone of *Panicum virgatum*, marking the deposit association, with relic bunches of *Panicum pseudopubescens* and *Carex umbellata*. The central basin is still bare and the lee slope is scarcely differentiated. A transect across this blowout is given in Table III.

TABLE III.—TRANSECT OF 20 QUADRATS, EACH 5 DM. SQUARE, ACROSS THE BLOWOUT SHOWN IN PL. VI, FIG. 1.

Linaria canadensis	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Panicum pseudopubescens	X	X	X	X	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-
Andropogon scoparius	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bouteloua hirsuta	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Festuca octoflora	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carex Muhlenbergii	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	
Carex umbellata	-	-	-	-	X	X	-	X	-	-	-	-	-	-	X	X	-	-	-		
Lespedeza capitata	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Croton glandulosus	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	X	-	-	-		
Aristida tuberculosa	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-
Ambrosia psilostachya	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-
Panicum virgatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	X	X	X		
Equisetum laevigatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	X		
Koeleria cristata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-		

The subsequent successions of vegetation depend primarily upon the physiographic changes. As the development of the blowout proceeds, the basin may begin to encroach on the windward slope. This is caused either by an increase in depth or by a general movement to the rear, or by both together. The sliding vegetation of the latter association reaches the bottom of the slope, is undermined and blown away, and its place is taken by plants of the basin. The windward slope thus comes to occupy a place intermediate in time between the basin and the *Panicum pseudopubescens* associations. If the basin is moving backward without an attendant increase in size, the lee slope will also extend backward over the extinct basin, constituting another succession. If the general movement is forward, the conditions are reversed and the basin association succeeds the blowsand association. This forward movement, however, reduces the grade of the windward slope, and eventually stops the settling of the sand. With this change in its environmental condition, stabilization begins, as will be described later, and the windward slope association is succeeded by the bunch-grass. So, while the basin may succeed the windward slope, the reverse does not take place.

Succession may also take place in either direction between the blowsand and the deposit associations. This depends in part on local environmental changes, leading to the increase in size of one association and the corresponding restriction of the other, but principally upon the direction of the general movement of the whole blowout. If forward, the blowsand association succeeds the deposit association; if backward, the reverse is true.

As has been previously mentioned, the basin of a blowout may eventually become so wide or so deep that further erosion by the wind is impossible. Erosion is the one factor of the environment which is chiefly responsible for the development of the basin association, and when that ceases the basin is at once replaced by a different type of vegetation. Some of the basin plants may persist for a time as relics. It seems probable that the first new vegetation is the blowsand association, mainly because of its proximity, its excessive seed production, and its rapid development. When the sand becomes stationary, it is no better suited to the blowsand plants than to a number of others, including bunch-grasses and perennials. These at once begin to colonize in the blowout and the stabilization of the basin is effected.

With the extinction of the basin the source is destroyed from which sand is added to the deposits, and they cease their growth. The surface of the sand, so far as it is not protected by the dune-

forming plants, remains more or less in motion and affords an environment suitable for the development of the blowsand association, which then becomes dominant. This condition is much like that on the broad flat deposits without dune-formers, where the rate of deposition is slow, because of the large surface to be covered, and the vegetation accordingly consists of the blowsand association. On the deposits this association persists longer than in the basin, because the greater exposure of the sand to the wind keeps it longer in motion. Finally the motion stops, and the deposits are also completely stabilized by various outside species, chiefly bunch-grasses. On the steeper slopes, held by *Rhus canadensis,* var. *illinoensis, Panicum virgatum,* or other species constituting the real deposit association, there is less opportunity for the development of the blowsand vegetation, because the perennials persist and retain their dominancy. They are finally joined by additional species, until eventually the surface is covered and the sand completely stabilized.

Summing up the successions within a single blowout (Figure 5), it is seen that there exists a perfect correlation between the vegetation and the physical conditions of the environment. The original *Panicum pseudopubescens* association is succeeded by each of the four blowout associations. Between these four, the successions depend partly upon the direction of movement of the blowout as a whole. The windward slope association may be succeeded by the basin association, but the reverse does not take place. Between the other three, the succession may be in either direction. The blowsand association shows a general tendency eventually to succeed both of the others, and may be regarded as the climax association of the blowout formation. This is directly correlated with the general dynamic effect of the wind, which leads, on the average, neither to erosion nor deposition, but merely to the movement of the sand. This condition is most favorable to the blowsand association, and is the cause of its dominancy It is probable that the blowsand vegetation would also appear on the windward slope after it has become static, but the relic bunch-grasses become at once the controlling feature, among which the blowsand species play a secondary part as interstitials.

When one blowout is filled by the deposits of another, or when secondary blowouts appear on the lee slope or deposits of an older one, there may be deviations from this normal series of successions. In the latter case the young blowout may be wholly or partially surrounded by a blowsand association, and the windward slope association is never developed because of the absence of any relic plants. When two or more blowouts unite to form a complex waste of sand,

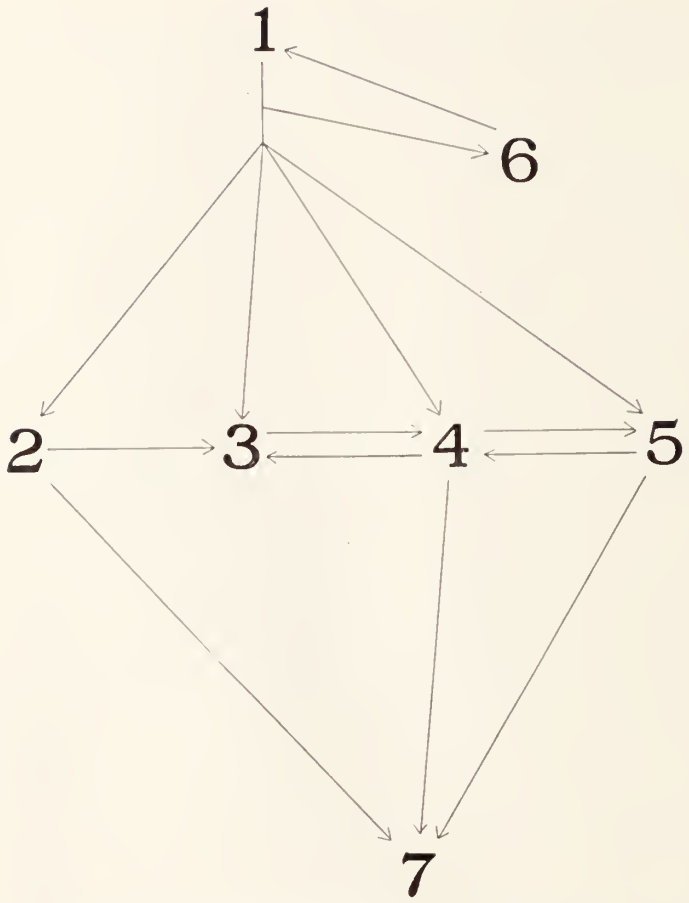

Fig. 5. Normal successional relations between the *Panicum pseudopubescens* (*1*), windward slope (*2*), basin (*3*), blowsand (*4*), deposit (*5*), *Hudsonia* (*6*), and bunch-grass (*7*) associations.

it becomes impossible to decipher the entire past history of the vegetation, but any of the successions given in the diagram between the basin, blowsand, and deposits may occur repeatedly, in any order, and for any length of time, until finally the sand becomes static and stabilization begins. The windward slope association alone is not included in the blowsand complex. It can follow only the *Panicum pseudopubescens* or more rarely the bunch-grass association, and if not succeeded by the basin association reverts to bunch-grass.

STABILIZATION OF THE BLOWOUTS AND THEIR REVERSION TO BUNCH-GRASS

Stabilization of the blowouts may take place in any or all of the four parts. Usually it begins on the windward slope and takes place last on the deposits. The windward slope is already occupied by bunch-grasses, although at a considerable distance apart. When the movement of sand ceases, other species invade the area at once and appear in large numbers between the bunches. *Aristida tuberculosa* and other members of the blowsand association are prominent but do not become dominant. Following them come *Oenothera rhombipetala* and *Lespedeza capitata,* making a thick weedy growth, and later various species of bunch-grass.

In the basin and on the lee slope stabilization begins with the extraordinary development of the blowsand association. It is followed immediately by large bunches of *Sporobolus cryptandrus* and by a rank growth of *Oenothera rhombipetala* and *Lespedeza capitata* (Pl. XI, Fig. 2). *Sporobulus cryptandrus* sometimes lives in actively blowing sand, but only in small depressed bunches (Hart and Gleason, *1907:* pl. XVIII, fig. 2). In partly stabilized blowouts it forms dense bunches one to two feet (3-6 dm.) wide and 1-1.5 ft. (3-5 dm.) high, surmounted by culms two or three feet (6-9 dm.) tall. Beneath the shelter of these three plants a number of interstitial species colonize, many of which are not common in the blowsand association. Some of these are *Hedeoma hispida, Polygonum tenue, Scutellaria parvula, Silene antirrhina,* and *Festuca octoflora.* This weedy growth lasts a comparatively short time. One blowout was observed where only about half as many plants of *Lespedeza* were growing as had grown the previous year, as shown by the dead stems. Since stabilization usually begins near the bottom of the blowouts, some may be found in which *Lespedeza* and *Oenothera* have already left the deepest part and occupy a ring around the sides. This also shows that the bunch-grasses which follow are not plants which slide in from the sides, as was intimated in an earlier paper (Hart and Gleason *1907:* 169). In this tangle the bunch-grasses gradually appear (Pl. X, Fig. 2), and by their growth restrict the interstitials, as was explained in connection with the bunch-grass association. Mats of *Antennaria, Cladonia,* and moss also appear very early. The perennials follow the bunch-grasses. The order of their appearance is not definite, but depends upon the composition of the neighboring bunch-grass association. Stabilization of the basin and windward slopes may take place at the same time, or there may be

a stabilized area behind the active basin, following it as it moves forward.

The flat open deposits without efficient dune-formers are stabilized in nearly the same way. *Paspalum setaceum* first becomes more abundant and is followed by large numbers of *Sporobolus cryptandrus,* with the usual growth of *Lespedeza* and *Oenothera.* Following these the bunch-grasses appear. A tract in the Oquawka area shows the results of twelve years of stabilization in this way. The field was formerly blowing actively, until some locust trees were planted as a windbreak at the west side. In the twelve years that have elapsed most of the blowouts have become extinct and the extensive flat deposits have been almost entirely stabilized. *Oenothera rhombipetala* and *Leptoloma cognatum* constitute the dominant species at the present time. The bunches of the latter are round and compact, but widely separate, and cover only about 30 per cent. of the ground. *Oenothera* is so abundant that when in bloom it shows almost a solid mass of color. But nine accessory species have appeared: *Paspalum setaceum, Ambrosia psilostachya, Bouteloua hirsuta, Croton glandulosus,* var. *septentrionalis, Cyperus Schweinitzii, Lepidium virginicum, Monarda punctata, Verbena stricta,* and *Physalis virginiana.* Proceeding up the lee slope from a partially active blowout toward this newly developed bunch-grass, the grasses appear in the following sequence: *Paspalum, Sporobolus, Leptoloma.* In this case the horizontal arrangement probably indicates the succesion in time as well.

THE HUDSONIA ASSOCIATION

In the Hanover area blowouts are sometimes stabilized by *Hudsonia tomentosa,* which forms a peculiar association of its own. *Hudsonia* grows in dense hemispherical tufts up to 4 dm. in diameter and is always gregarious, occupying 10 to 50 per cent. of the whole surface. It can not endure burying and does not possess the power of growing up with the deposition of sand. Consequently it does not live on deposits. Similarly it can not well resist undermining and does not live in basins or on windward slopes. Neither has it been observed on actively moving lee slopes, nor is it able to hold its own in competition with bunch-grass. Its optimum habitat seems to be open quiet sand, and it is restricted therefore to young blowouts in which the surface is nearly flat and the sand is not actively in motion, or to small portions of more active blowouts where it is able to get a foothold. The plants appear first at the

edge of the bare sand and soon cover the whole area. When a colony is once established it effectually checks any further movement of the sand. Colonies in young blowouts are usually surrounded by *Panicum pseudopubescens,* which soon closes in and reoccupies the space. A few plants of *Hudsonia* may persist for a time, but their life is short. But few other species occur in the association. Those observed are *Cassia Chamaechrista, Euphorbia corollata, Polygonella articulata, Carex umbellata,* and *Andropogon scoparius.* The last two are probably pioneers in the redevelopment of the *Panicum pseudopubescens* or bunch-grass association.

Successions from the Blowout Formation

As the blowouts increase in size and become progressively deeper the movement of the sand becomes less active, and in nearly every case they finally become stabilized and revert to the bunch-grass association. The few cases where the reversion does not take place are of interest, since they illustrate a peculiar series of successions and introduce some associations not found elsewhere in the sand regions under discussion.

The general vegetational and environmental conditions of one type of these successions have been given by Gleason (*1907:* 167-169) from observations on a few blowouts in the Havana area. The principal changes in the ecological conditions are in the direction of protection against wind, resulting in a stable substratum, and a larger supply of water, depending upon the depth of the blowout. These conditions, rather unusual for the sand areas, permit the development of a more mesophytic vegetation. This is generally simply a more luxuriant growth of bunch-grass composed of the usual species. More rarely entirely different species appear, especially if there are groves or cultivated grounds near.

The Blowout Thicket Association

A simple case, leading to what may be named the blowout thicket association, is shown in a blowout near Oquawka. The blowout is nearly stabilized, with the usual growth of *Lespedeza* and *Oenothera,* but in the very bottom two locust trees (*Robina Pseudo-Acacia*) have become established. Under them are plants of *Oxybaphus nyctagineus, Lactuca canadensis,* and an unknown grass, of a species not occurring in the surrounding bunch-grass. In another blowout several young plants of *Populus deltoides* are growing (Pl. XI, Fig. 2). In a similar deep blowout in the Hanover area is a large tree

of hackberry, *Celtis occidentalis,* probably forty or fifty years old. Under it are shrubs of apple, *Cornus Baileyi,* and *Rosa* sp. They are overhung with vines of *Psedera quinquefolia,* and in their shade are plants of *Polygonatum commutatum.* Many other common sand plants are associated with them. It is probable that all these species were introduced by birds, since they all have fleshy fruits. *Vitis vulpina, Menispermum canadense, Populus deltoides,* and *Acer Negundo* were reported by Gleason (Hart and Gleason, *1907:* 168) for similar conditions in the Havana area.

Although these three blowouts have no species in common, the vegetation probably represents the first stages, changed considerably by proximity to civilization, of a definite series. This series, however, has always been curtailed by refilling the blowouts with sand, since there is no association in the three areas mentioned which can possibly be referred back to this origin.

THE STENOPHYLLUS ASSOCIATION

It has already been mentioned that a thin layer of loamy soil is formed on the surface of the sand in the bunch-grass association. This layer is coherent and quite resistant to wind action. The deposits of a blowout may bury this soil layer to a considerable depth and for an indefinite time, completely destroying the original vegetation. At a subsequent period another blowout may develop on these deposits and finally expose the old soil layer. When this is uncovered the growth of the blowout in depth ceases. Its future growth, if any, is lateral, leaving a flat bottom which is level or gently sloping. Blowouts of this type are generally easily recognized by the bottom being flat instead of the usual concave shape. As soon as the soil layer is uncovered a new type of vegetation appears, characterized particularly by the small sedge *Stenophyllus capillaris,* and constituting the *Stenophyllus* association.

This is well illustrated by several blowouts in the Hanover and Oquawka areas. One in the former (Pl. XI, Fig. 1) is of special interest since it shows the old soil over the western half of the blowout, while the other half is still pure sand, with the usual vegetation. The western half is flat, but slopes up about one foot (3 dm.) in its total width of 25 feet (8 m.), indicating the gently rolling nature of the original surface. The soil layer is covered with one to two inches (2-4 cm.) of fresh sand, blown in from an active blowout toward the west. This portion of the blowout is occupied by numerous small tufts of *Stenophyllus* about an inch (2-4 cm.) wide, a

square foot containing on an average from 75 to 100 plants. Associated with it are numerous plants of the blowsand association: *Diodia teres, Aristida tuberculosa, Croton glandulosus,* var. *septentrionalis, Linaria canadensis, Mollugo verticillata, Cyperus Schweinitzii,* and *Euphorbia corollata.* The presence of these accessory species is probably correlated with the thin deposit of fresh sand, since they are not found on the soil layer proper. A blowout of the same type in the Oquawka area (Pl. XI, Fig. 2) is about 80 by 100 feet (25 by 30 m.) in size, but less than three feet (1 m.) deep. Most of the broad flat basin is covered with a black crusted soil layer and occupied by large numbers of *Stenophyllus* and a few plants of *Gnaphalium polycephalum* and *Lactuca scariola,* var. *integrata.* There are also two circular patches of an unknown moss, probably only two or three years old. Parts of this basin are still covered with a thin layer of sand, on which the vegetation is the usual blowsand association, characterized especially by *Cenchrus carolinianus, Froelichia floridana,* and *Paspalum setaceum.* Stabilization has already begun with *Lespedeza capitata* and *Oenothera rhombipetala,* and at one end are a few plants of *Populus deltoides.*

It seems probable that this association is finally succeeded by a prairie vegetation, although no evidence of this was seen during the present investigation. According to Gleason (Hart and Gleason, *1907:* 168) it may be followed in the Havana area by *Cladonia* and *Antennaria,* and later is converted into "prairie, scarcely distinguishable, in vegetation at least, from the typical prairies of central Illinois."

The Swamp Formation

the salix and solidago associations

Blowouts may become so deep that they reach and uncover moist layers of sand, probably not far above the water-table. In these, new plant associations soon appear, which may be even hydrophytic in nature. The few cases observed have not made it possible to determine the order in which the vegetation develops, and the discussion must be limited mainly to the simple description of conditions as they are. Cowles has mentioned a similar succession at the head of Lake Michigan (*1899:* 308).

The deepest of the excavations, measured by the vegetation rather than by actual dimensions, is in the "Devil's Neck" north of Topeka, in the Havana area. The center of the depression is a sandy loam and probably represents the subsoil, the Miami loam of

the Soil Survey, on which the sand is superposed. It is occupied by a sparse vegetation of *Ludvigia palustris* and *Eleocharis obtusa*. Surrounding it is a zone of *Salix longifolia*, now about three feet (1 m.) high, and *Juncus acuminatus*. Outside of this are the usual plants of stabilized blowouts, particularly *Oenothera rhombipetala* and *Lespedeza capitata*. This vicinity was studied also in the summer of 1904, and according to the best recollection of the writer, no such assemblage of plants was observed. It is entirely probable that the association has developed since that time. Willow seeds may easily have been blown in by the wind, and the seeds of the herbaceous plants may have been brought in in mud on the feet of birds, which were attracted by a temporary pool of water collected after rains.

Not far from this depression there was a similar one, but with sandy bottom. In 1904 it was occupied by *Polygonum acre*, *Hypericum mutilum*, *Cyperus rivularis*, and *Juncus tenuis*. In 1908, after a lapse of four years, the deepest part of the depression had been filled, so that the bottom was generally level. The prevailing vegetation is blue-grass, *Poa pratensis*, but a few relics of *Hypericum*, *Juncus*, and *Cyperus* still persist.

Just east of Havana, at the "Devil's Hole," there is another deep depression with a more luxuriant growth of vegetation. In the deepest part there is a small but dense thicket of *Salix longifolia*. Under the willows the sand is covered with a carpet of moss and decaying leaves, making a humus layer which must aid greatly in the absorption and retention of water. At the edge of the thicket is a narrow zone of *Boehmeria cylindrica*, *Ludvigia alternifolia*, and *Lycopus americanus*. These plants may be considered as a part of the *Salix* association but do not live within the thicket because of the weak light. Around the willows, and extending partly up the hill, is a dense growth of *Solidago graminifolia* and *Equisetum hyemale*, var. *intermedium*, constituting the *Solidago* association. The two alternate. *Equisetum* occupying about one third of the zone. Mingled with these are a few plants of *Cacalia atriplicifolia*, *Vernonia fasciculata*, and *Asclepias syriaca*, as well as a number of the usual blowsand plants, as *Paspalum setaceum*, *Cassia Chamaechrista*, *Cristatella Jamesii*, *Croton glandulosus*, var. *septentrionalis*, *Ambrosia psilostachya*, and *Monarda punctata*. *Eragrostis trichodes*, *Chrysopsis villosa*, and *Lithospermum angustifolium* also occur, but are rare. This zone has a vertical width of about six feet (2 m.). Near its upper (outer) margin are a number of old bunches of *Sporobolus cryptandrus* and a few of *Andropogon fur-*

catus and *Panicum virgatum*. These, as well as the appearance of the goldenrod, indicate that the zone is migrating up hill over the partially stabilized sand. The rounded contour of the willow thicket with the youngest plants at the edge, show that it is also enlarging and occupying successively higher levels. This movement is correlated with the development of the retentive layer of humus under the thicket, but the movement of the *Solidago*, already six feet (2 m.) above the willows, depends more upon the general vegetative activity of the plant itself.

These two associations, *Solidago* and *Salix*, may then be expected to appear in any deep blowout. Naturally the deeper ones only can support the willow, which requires a larger supply of moisture. This zonal relation of willow and goldenrod is by no means local, but may be observed in many localities in the eastern states. The absence of the goldenrod zone around the willows in the first depression described is merely one of those chance instances of distribution for which no explanation can be given. Possibly the presence of *Juncus acuminatus* indicates the first stage in its formation.

It is evident that with the establishment of the dense growth of *Solidago* the movement of the sand must cease, and it may be that it does not appear until the sand has first become static. In either case, if its depth is not sufficient to reach moist layers of sand the willow can not develop and the blowout will be occupied by *Solidago* alone. On the other hand, if the conditions are suitable for the growth of willows, the *Solidago* association can develop simultaneously around it. The willows therefore, requiring the deeper excavation, can not follow the goldenrod, but must appear before or with it. When both are established, the former becomes dominant because of its greater control of the physical conditions and tends to succeed the latter.

This condition of affairs is peculiar in two respects. First, the development of the dominant *Salix* association can not follow in time that of the minor *Solidago* association. Second, the general movement of the zones is centrifugal, extending progressively further up the sides of the blowout, and the direction of succession is apparently toward a hydrophytic climax.

It must not be presumed that in this case a hydrophytic climax will appear. It is probable that the water-retaining humus does not become thick enough to hold standing water, and it is still more probable that a new movement of sand from the west may overwhelm the whole association. As in another case already mentioned, there is at present no association in the region that could possibly be

referred back to this for its origin, indicating that all former associations of this type have sooner or later been destroyed.

THE POLYTRICHUM ASSOCIATION

In the Dixon area the hydrophytic series is carried further, and a new association, characterized by *Polytrichum juniperinum*, also appears. The *Solidago* and *Salix* associations are also represented. In all, six depressions show one or more of these associations and illustrate not only the successions between them but their development as well. For convenience they will be referred to by letters. These depressions are near the Northwestern tracks about four miles west of Dixon. Blowout *A* is on the north side of the track; *B* is near the track on the south side; *C* is east of the deposits of a large blowout south of the track; *D*, *E*, and *F* are in this blowout or its southern extension.

Blowout *A* is a shallow depression, but with rather moist sand. It is occupied mainly by a dense growth of *Solidago graminifolia*, with *Equisetum arvense*, *Carex* sp., and *Spiraea salicifolia* as accessory species.

Blowout *B* is smaller in width and length, but deeper and with steeper sides. On the outside there is a ring of *Solidago graminifolia* with an abundant growth of *Aristida tuberculosa*. The most abundant accessory species is *Lespedeza capitata*, and others of less frequency are *Andropogon furcatus*, *Cassia Chamaechrista*, and a few sterile grasses which could not be identified. *Aristida* and *Solidago* are almost equally abundant except at the inner margin, where the former is slightly in excess. This zone extends up the hillside to the typical bunch-grass and is rather sharply delimited from it. In the center of this ring is the *Polytrichum* association. The moss grows in dense mats, occupying all the surface in the deepest part of the depression. These mats are very thick and spongy and sink beneath the feet several inches. The dead stems grade off beneath into a thick, brown, moist, spongy layer of a somewhat peaty texture. The mats are sparsely occupied by solitary plants of the several accessory species. *Solidago graminifolia* is the most abundant of these and extends entirely across, but the plants are much smaller than in the association outside. The others are *Lycopus americanus*, *Hypericum majus*, *Salix pedicellaris*, and *Aster* sp. There are also a few depauperate relic bunches of *Panicum virgatum*. There is a narrow tension zone between the two associations, in which the mats of moss are less close and the stand of *Solidago* less pure. The moss is

encroaching upon the *Solidago*. There is a difference of about 1.5 feet (5 dm.) in the upper and lower levels of the *Polytrichum* zone, and the *Solidago* association is somewhat broader vertically. The deepest part is about 16 feet (5 m.) above the drainage level 200 yards (200 m.) away and all the intervening territory is sand. The mesophytic nature of the association must be due to the action of the moss in developing a retentive layer of humus, rather than to any feature of drainage.

Blowout *C* is small and flat and most of it is occupied by a dense carpet of *Polytrichum*, with many low shrubs of *Salix pedicellaris* and some seedlings of *Populus deltoides*. The surrounding zone consists chiefly of *Solidago graminifolia* and *Lespedeza capitata*. This blowout is about 12 feet (4 m.) above the drainage level and about 6 feet (2 m.) above the cultivated field just east of it. It is 14.5 ft. (4.8 m.) below the crest of the deposits of blowout *D* at the west.

D is a large blowout still active on the north, east, and west. A low oblong area enters the blowout from the southwest and is now almost entirely stabilized. Most of this represents a recent deposit of sand from the rear, but the deepest part, nearest the center of the blowout, is the extinct basin. It is now 11 ft. (3.3 m.) below the crest of the deposits. In this basin both the *Salix* and *Solidago* associations are now developing. The latter is represented by a plentiful growth of *Solidago graminifolia* and *Aristida tuberculosa*, with some *Juncus acuminatus*; the former by abundant young plants of *Salix longifolia*, with *Ludvigia palustris*, some small plants of *Panicum virgatum*, four or five plants of *Populus deltoides*, and four bunches of *Scirpus cyperinus*. The sand is wet and well covered with a layer of dead vegetable matter.

On pure sand back of this basin and 6-12 inches (1-3 dm.) above it is a mixture of the *Solidago* and *Polytrichum* associations. The ground is partially covered with dense or open mats of *Polytrichum*, with *Hypericum gentianoides*, *Rhexia virginica*, *Juncus acuminatus*, *Polygala sanguinea*, and seedlings of *Salix pedicellaris*. *Solidago graminifolia* and *Aristida tuberculosa* are abundant, but as usual are conspicuously smaller when growing on the moss mats. *Rhexia* may live in the middle of the mats, but *Hypericum gentianoides* grows only in the bare sand in the immediate vicinity of the moss.

Each of these parts of the blowout illustrates early stages in the development of the associations, before their zonal relations have been established. The *Salix* association apparently demands moist

sand and comes in only in the deepest part of the blowout. *Polytrichum,* on the other hand, may colonize in relatively dry sand, where it at once produces moist conditions by its dense growth.

Still farther in the rear and also somewhat higher is a deposit of sand representing a later stage in the refilling of the basin. It has been stabilized by *Panicum virgatum* and *Lespedeza capitata.* Besides these, *Solidago nemoralis, Hudsonia tomentosa,* and *Panicum pseudopubescens* indicate a reversion to bunch-grass. Over this whole area mats of *Polytrichum* are appearing. Some mats are large, confluent, and dense; others small, regularly circular, and with very small plants near the margin. These are coming in everywhere, even under the bunches of *Panicum virgatum* and *Panicum pseudopubescens,* or surrounding *Hudsonia tomentosa* or *Solidago nemoralis.* Coming up with it are many plants of *Solidago graminifolia, Aristida tuberculosa, Rhexia virginica, Polygala sanguinea,* and in the deepest parts a few plants of *Scirpus cyperinus.* On the larger and older mats these species are small or absent, and other species more characteristic of the association occur. These are *Salix pedicellaris, Viola lanceolata,* and *Spiranthes cernua.* A few depauperate plants of *Panicum pseudopubescens* persist even in the dense mats of the moss. Along the south and west margins of this area almost pure mats of *Polytrichum* extend to the very edge of the blowsand (Pl. XII, Fig. 1; XII, Fig. 2), reaching a height of three feet (9 dm.) above the *Salix* association already described. They are associated only with the three typical species just mentioned. Throughout this area *Solidago graminifolia* and *Aristida tuberculosa* occur, but they are most abundant on the bare sand between the mats. As the *Polytrichum* increases and finally occupies all the surface, these will be forced into a marginal zone, as in blowouts *B* and *C.*

THE SWAMP ASSOCIATION.

In the Dixon area, just south of blowout *D,* is a long north and south excavation (Pl. XIII, Fig. 1), with rather steep walls of bare sand on either side. These walls represent a partially stabilized windward slope, and are occupied by *Carex umbellata, Aristida tuberculosa, Panicum pseudopubescens,* and *Solidago nemoralis.* In the deepest parts are two ponds, *E* and *F,* surrounded by definite zones of vegetation. The bottom of the ponds is a black muck well mixed with sand. The water-level fluctuates with the weather. When visited in August it was one foot (3 dm.) above the basin of blowout *D,* 6.4 feet (2.1 m.) above the country to the east, and 16 feet (5.4 m.)

above the drainage level at the northeast. The inner zone of vegetation is characterized by *Scirpus cyperinus, Eleocharis obtusa, Ludvigia palustris, Juncus nodosus,* and a few relics of *Panicum virgatum.* Outside this is a regular but narrow zone of *Polytrichum,* with *Polygala sanguinea, Juncus acuminatus, Hypericum gentianoides,* and *Rhexia virginica.* Next is the zone of *Solidago graminifolia* with its usual associate *Aristida tuberculosa,* and, as accessory plants, *Rhexia virginica, Juncus acuminatus, Gerardia purpurea,* and *Polygala sanguinea.* Either of these outer zones may be absent for short intervals, but are usually very distinct.

The second pond, *F,* was almost dry when visited in August, 1908, and its mucky bottom was about 15 inches (4 dm.) below the water-level in pond *E.* Its vegetation had been badly destroyed by cattle.

On the windward slope near *E* a mat of *Polytrichum* is developing in a very shallow, flat depression three feet (9 dm.) above the water-level and one foot (3 dm.) above its nearest neighbors. It is surrounded by a large patch of *Hypericum gentianoides* extending one to ten feet beyond it.

From this detailed description it is seen that the vegetation of the foregoing series of depressions of the swamp formation comprises four associations of the following species.

1. The *Solidago* association. *Solidago graminifolia, Aristida tuberculosa, Equisetum arvense, Spiraea salicifolia, Carex* sp., *Polygala sanguinea, Gerardia purpurea, Juncus acuminatus, Rhexia virginica.* Accessory or relic species: *Stenophyllus capillaris, Lespedeza capitata, Andropogon furcatus, Cassia Chamaechrista.*

2. The *Salix* association. *Salix longifolia, Salix nigra, Populus deltoides.* Accessory or relic species: *Panicum virgatum, Scirpus cyperinus, Juncus acuminatus, Ludvigia palustris.*

3. The *Polytrichum* association. *Polytrichum juniperinum, Hypericum gentianoides, Salix pedicellaris, Aster* sp., *Lycopus americanus, Hypericum majus, Viola lanceolata, Rhexia virginica, Spiranthes cernua.* Accessory or relic species: *Polygala sanguinea, Panicum virgatum, Juncus acuminatus, Ludvigia palustris.*

4. The swamp association. *Scirpus cyperinus, Juncus nodosus, Eleocharis obtusa, Ludvigia palustris.* Relic species: *Panicum virgatum.*

The *Salix* and *Polytrichum* associations occupy parallel positions, but develop under different conditions. The former demands a considerable supply of moisture and is restricted to the deeper depressions, whereas the latter may develop at almost any level in the blow-

out. The appearance of the *Salix* association can not follow in time that of the *Solidago* association, as has already been explained. *Polytrichum* may colonize not only under the *Solidago* but also under a more xerophytic type of vegetation as well. Both indicate moist sand; the mosses by retention of moisture, the willows by retention and depth of position. Consequently each develops contemporaneously with the *Solidago* association, and in the early stages the associations are not differentiated. Later the *Solidago* association is forced to the outside.

In both cases the succession is in a xerophytic-hydrophytic direction. Nothing has been observed to succeed the *Salix* association, even in the oldest and deepest blowouts. The mats of *Polytrichum,* on the other hand, produce a peaty layer over the sand, which becomes so thick that it retains standing water and admits of the development of a pond society. These ponds must be held by a water-tight bottom, otherwise their water would soon drain out through the sandy subsoil. As it is, they are conspicuously higher than the general level of the country. The zones surrounding the ponds move outward and upward and permit the continued growth of the pond. This is evidenced not only by the position of young mats of *Polytrichum,* but also by relic bunches of such typical sand plants as *Panicum virgatum,* now actually in the standing water. If continued far enough the increase of the pond might ultimately lead to the establishment of other associations, such as pondweeds or water-lilies. Its growth is retarded, however, by the gradual deposition of wind-blown sand, by the accumulation of soil by the aquatic plants, and by loss of water because of increased pressure on the mucky bottom. Most important of these is the deposition of sand, which will mix with the peat and eventually raise the level of the soil somewhat above the water-table. The later stages in the succession are probably similar to the meadows in the Kankakee area, except that the latter represent primary successions on a large scale, instead of secondary successions in a small area.

Succession of the Prairie Formation by the Forest

It was a matter of great interest to the first explorers and settlers in Illinois that so much of the surface was occupied by prairie, and that the forests were confined to certain physiographic divisions, especially the stream valleys. In seeking to account for this natural feature, the earlier generation of scientists, and to some extent even the modern ones as well, were influenced, or even prejudiced, by two

wrong ideas. In the first place, as they and their ancestors had lived for generations in a forested country, the forest came to be regarded as the only possible natural covering, and any other type of vegetation was considered extraordinary. In the second place, they did not at first recognize that the forests were everywhere encroaching slowly upon the prairies, or that the encroachment became measurable as soon as the prairie fires were checked. The prairie is not an extraordinary thing, to be explained only by some strange or fanciful causes; it owes its origin to ages of arid climate in the west and southwest (Harvey, *1908:* 84). The forest also owes its origin to ages of humid climate in the east and southeast (Adams, *1902*). These great climatic types acting upon the plant world through evolution and elimination, gradually developed the two extreme types of vegetation, each of which was especially adapted to its own environment. After the close of the glacial period migration of each of these types brought them in contact in Illinois and the neighboring states, and a struggle for supremacy began between them. The outcome is decided mainly by two sets of factors; first, the control of the environment by the vegetation, and second, the climatic conditions of temperature and rainfall. In the first case, the prairie vegetation, by virtue of its close sod, tends to prevent the proper germination and growth of the forest-tree seedlings (Harvey, *1908:* 86; Robbins and Dodds, *1908:* 35). Prairie fires, following the advent of man, also tend to restrict the growth of the forest. On the other hand, the forest has control of the light supply for the herbaceous layers and the well-established trees are resistant to fire. Above all, the climatic conditions are favorable to forest (Schimper, *1903:* 162-173; Transeau, *1905*). The balance has been in general in favor of the forest and it has advanced slowly upon the prairie.* The greatest speed of advance has been along the lines of least resistance, the watercourses, and has resulted in long strips of forest, paralleling the streams, and usually widest on the east side of streams or marshes where they were better protected from fire. In the sand regions the forest distribution is not regulated in that way, because of the absence of small streams, but it does show a possible relation to fires. Where the sand lies in disconnected ridges, separated by strips of moist or swampy ground acting as fire-breaks, as in the Havana, Ambov, and Kankakee areas, there is a good growth of forest on the higher ground. Where the sand lies in large continuous masses, as in the

* It is probable that at certain places and during certain periods the influence of fires has turned the balance in favor of the prairie, but this has not interfered with the general advance of the forest.

Oquawka and Hanover areas, there are large tracts of prairie. The Winnebago area lies protected on three sides by streams of considerable size, and is almost entirely forested, except the cultivated fields.

In the Havana area, there is a belt of forest along the Illinois river, and large forest masses at the south and north ends, particularly near Forest City and Kilbourne. In other parts of the territory the broader deposits of sand are usually prairie, and the forest is restricted to the narrow ridges. These extend north and south and mark the location of old sand-bars. In the Amboy area the distribution is similar, but the ridges run generally east and west. They have probably all been forested except those nearest the margin of the deposits. In the Oquawka area there is a belt of forest along the Mississippi river and another inland near the bluff line. These are connected by broad bands of forest which separate several areas of prairie. The Hanover area has a similar belt along the Mississippi, and a number of transverse strips extend inland. These have been partially cleared, but probably none of them crossed to the bluffs except at the extreme northern end. The Winnebago area was entirely forested except a few small areas of marsh and islands of prairie. It is difficult to estimate the proportion of the area covered with forest. It was probably considerably more than half in the Oquawka area, about a third in the Hanover area, and about a half in the Havana area.

The regular belt of forest along the rivers in the last three areas may be correlated with the effect of fire. The transverse bands across the area in the Hanover and Oquawka areas follow the most irregular portion of the surface, where the effect of fire was possibly limited. The large grove northwest of Hanover station, in particular, follows a line of steep-sided irregular dunes totally unlike the gently rolling prairie.

The encroachment of the forest is caused by the slow migration of the forest trees in every direction. The open structure of the bunch-grass does not prevent the proper germination of seeds or growth of seedlings as does the close sod of a normal prairie. Few species of trees, however, are able to withstand in their seedling stages the extreme conditions of the physical environment. These are especially the shifting nature of the sand, the hot surface layer, which may be almost totally dry to a depth of more than a decimeter, and the lack of protection against wind during the winter. Still another restricting influence is the absence of ready means of dispersal. The trees composing the early stages of the forest are oaks. Their heavy acorns have no means of dispersal except gravity and

the agency of animals. There are few animals to carry the acorns out on the prairie. The majority of such acorns are eaten, and many of the remainder decay. Some trees produce exceedingly heavy crops of acorns, which lie in layers an inch or two (3-4 cm.) deep beneath the tree, but of a large number examined, not one was sound. The life of a tree seedling is at best precarious, and in an unusual environment, with full exposure to wind and sun, few of them may be expected to survive. It is possible that some seasons are more favorable than others, and that after intervals of several years a succession of two or three favorable seasons may lead to a considerable extension of the forest. This condition has been described by Ramaley (*1908:* 30) and is probably of wide application.

Establishment of the forest makes at first very little difference in the environment. The trees are relatively far apart, and sufficient light comes through the foliage to permit the growth of many species of the original bunch-grass. The edge of the forest, therefore, shows, not a change in the flora but merely the addition of a few other species. There are at present few places where the contact between forest and prairie can be observed. Of these, the best is in the Hanover area (Pl. XIII, Fig. 2). The ground cover is the usual climax growth of the mixed consocies of bunch-grass, consisting particularly of *Koeleria cristata* and *Andropogon scoparius.* With these are *Bouteloua hirsuta, Aster linariifolius, Aster sericeus, Callirhoe triangulata,* and other common species. The sand is in apparently the same condition as upon the prairie. The fallen oak leaves have either blown away completely or have been collected in piles around fallen branches and in thickets of *Rhus canadensis,* var. *illinoensis.* There is none of the additional herbaceous species typical of the older established forest. In the Winnebago area there are a few small open spots within the forest, which represent the last stages of a prairie. In the first of these there are *Carex Muhlenbergii, Koeleria cristata, Liatris cylindracea, Lespedeza capitata, Viola pedata, Polygala polygama,* and *Artemisia caudata.* Oak seedlings one or two years old were also present. In a larger opening (Pl. XVII, Fig. 1) the prairie character is more obvious. The dominant species consist of a mixed growth of *Panicum Scribnerianum, P. perlongum, P. pseudopubescens, P. virgatum,* and *Carex Muhlenbergii.* Between their branches the ground is well matted with *Cladonia.* Some of the accessory species are *Tephrosia virginiana, Amorpha canescens, Lespedeza capitata, Solidago nemoralis, Asclepias amplexicaulis, Potentilla arguta, Acerates viridiflora,* var. *linearis, Viola pedata,* and *Ambrosia psilostachya.* There are no forest relics.

This fact, together with the pure yellow sand of which the substratum is composed, indicates that it never has been forested.

The boundary between the forest and prairie differs from the usual forest margin in the absence of a tension zone and a definite vegetation. Thickets of hazel, of sassafras, or of sumach, which surround the typical Illinois forests, are absent. There is no sharp distinction of flora within and without the forest edge, and no massing of a large number of species near the margin. The whole succession is of a type rarely mentioned or described, in which there is at first no essential change in the environment.

There is no first-hand evidence concerning the rate at which the extension of the forest is proceeding. The first settlements were usually made near the edge of the forest, where clearing and cultivation at once stopped any advance. Historical evidence is not always of value, because complete dependence can not be placed on statements of a scientific nature made by travelers or casual observers. A note by Patrick Kennedy (Imlay, *1797:* 508), however, is suggestive, and probably at least partially correct.

"About sun-set we passed the river Demi-Quian.* It comes in on the western side of the Illinois river (165 miles from the Mississippi); is 50 yards wide, and navigable 120 miles. We encamped on the south-eastern side of the Illinois river, opposite to a large savanna, belonging to, and called, the Demi-Quian swamp. The lands on the southeastern side are high and thinly timbered; but at the place of our encampment are fine meadows, extending farther than the eye can reach, and affording a delightful prospect. The low lands on the western side of the Illinois river extend so far back from it, that no high grounds can be seen. Here is plenty of buffalo, deer, elk, turkies, etc."

Kennedy's whole narrative seems reliable, and we may believe that at least in some directions his camp commanded an uninterrupted view of the prairie. At the present time, however, the marginal belt of timber along the river in the vicinity of Havana is from 100 yards to a quarter of a mile (100 to 500 m.) wide, while the fringing woods along Quiver creek and large tracts of black oak completely cut off a view of the prairies. If Kennedy's statement is correct, then large areas of timber have developed within the last century.

It is difficult to explain the migration of the oaks. Their normal method is by gravity, which tends to scatter the acorns to a little distance as they fall from the trees. By this method alone the mi-

* The Spoon river, which empties into the Illinois opposite Havana.

gration even of a few miles would require thousands of years. The animals which feed upon acorns do not usually carry them a long distance, and those which are carried away are generally eaten. The acorns are produced in large numbers and lie thickly on the ground beneath the trees, but, as reported also by Britton (*1903:* 578), most of them are not viable. Reid (*1899:* 29) reports that in England rooks carry acorns to some distance and that isolated young plants may be found at a considerable distance from fruit-bearing trees. It is his idea (*1899:* 31) that the "accumulated accidents of some thousands of years" are sufficient to explain the distribution of oaks in England. In the Illinois sand region seedling oaks are always few in number and are never found on the prairie. Accidents can not be invoked here to explain a migration so regular, so continuous, and apparently so rapid, and the whole question must be left unanswered.

When once established the forest is permanently dominant, unless destroyed by man or by some exceptional physiographic changes. In the former case there may be a temporary reversion to the bunch-grass association. One such case was observed near Forest City, in the Havana area. The ground was occupied by a good growth of bunch-grasses, including *Panicum pseudopubescens*, *Leptoloma cognatum*, *Sorghastrum nutans*, *Andropogon scoparius*, *Tridens flavus*, *Boutcloua curtipendula*, *Paspalum setaceum*, and *Carex Muhlenbergii*. There were thickets of *Rhus canadensis*, var. *illinoensis*, and mats of *Opuntia Rafinesquii*, and numerous interstitial plants of *Cassia Chamaechrista*, *Ambrosia psilostachya*, and *Monarda punctata*. None of the perennial group was present. Numerous young plants of *Quercus marilandica* and *Quercus velutina* were appearing, indicating the approaching end of the bunch-grass association.

Within the forest may be distinguished two well-marked associations, related to each other by a clearly defined order of succession, and differing in their habitat and component species. Of these the pioneer is the black oak association.

The Forest Formation

The black oak association

The associations of the forest formation are fewer in number than those of the prairies. The first of them in order of succession and the most typical of the sand region is the black oak association. (Pl. XIV, Figs. 1, 2; XV, Figs. 1, 2; XVII, Fig. 1). It is found

in each area studied, except the Dixon area, which is entirely without forest. In the others most of the forested portion is covered with this type. It has also a wide distribution beyond Illinois and is mentioned under the same or different names by several writers.

Cowles described the association (*1899:* 379-382) at the head of Lake Michigan under the name of oak dunes. Nearly all the herbaceous species mentioned in his short list occur also in Illinois. Jenning's *Quercus velutina-imbricaria* Forest Formation of Cedar Point (*1908:* 300) is similar, but includes many plants which represent a somewhat later stage in succession. The oak-pine-sassafras society of Livingston (*1903:* 40-42) in Kent county, Michigan, is also much like the Illinois association, but contains many relic specimens of the pine forests which preceded it in order of succession. Britton (*1903:* 578, 579) mentions the occurrence of black oak on the sand-plains of Connecticut. He did not differentiate a particular association, but it is very probable that at least some of the vegetation is of this type.

In each of the extralimital localities mentioned the dominant tree is the black oak, while the herbaceous vegetation shows a considerable variation. This is because of the differences in the neighboring associations, from which many species find their way into the black oak forest. Warming (*1909:* 146) has termed such conditions *geographical variations* of an association. With our present knowledge of plant associations it is not clear how much weight should be given to these variations in floristic composition.

The association is characterized by the black oak, *Quercus velutina,* and in the Havana and Oquawka areas also by the black-jack oak, *Quercus marilandica.* Both species have the same general habit and live together in various proportions, but with the black oaks usually more numerous. The trees are sometimes close and crowded, sometimes wide apart. Old forests, whose origin probably dates back to the period of prairie fires, and forests on steep dunes are usually open, with trees 5-20 yards (5-20 m.) apart. Young forests of recent development or those protected by swamps are usually dense, with an average distance of 3-15 ft. (1-4 m.) between the trees (Pl. XIV, Fig. 1). Densest of all are the young groves which have recently sprung up in abandoned fields and clearings. In these the trees stand at close intervals and the trunks are covered with stiff, crooked, dead branches down to two or three feet (1 m.) from the ground (Pl. XIV, Fig. 2), making them almost impassable. The older and more open forests are especially characterized by bare crooked trunks with divergent branches at a height of 6-12 ft. (2 to 4 m.).

This gives the grove an aspect not unlike an old apple orchard (Pl. I, Fig. 1). The absence of low branches is possibly due to the action of fires, since natural pruning does not seem very effective. The trees are uniformly low, rarely exceeding 35 ft. (10 m.) in height or one foot (3 dm.) in diameter. In the Havana and Oquawka areas the bitter nut hickory, *Carya cordiformis,* also occurs.

Since the oak trees are the dominant members of the association, they determine to a large extent the ecological nature of the forest floor, and many peculiarities in the growth or distribution of the herbaceous or shrubby members are directly correlated with the character of the forest. In the young oak woods the ground is bare sand, covered by leaves only around fallen branches or sumach thickets. In forests of greater area or wider extent there is a greater accumulation of leaves, leading to the formation of a thin layer of leaf-mold. The thickness of the leaf-mold is a crude index to the age of the forest. The surface layers of sand thus gradually attain a greater capacity for holding water and a greater amount of organic matter. Even in the young forests the surface layers of sand are in general moister than on the prairie, because of the lower intensity of light and the slight exposure to the wind. The intensity of the light is much reduced, although the foliage of the trees is less dense than in the more typical forests of the state. These two features, soil and light, are the most important environmental factors in the association.

The herbaceous and shrubby vegetation, after a few ubiquitous weeds and naturalized plants are excluded, may for convenience be referred to two groups. The prairie group includes those species more abundant in and more typical of that formation, and the forest group includes species more characteristic of the forest and rare or absent in the prairies. It is impossible, but also unnecessary, to draw a sharp line between the two groups. It is evidently the light relation that determines the distribution of the members of the prairie group, since they occur in leaf-mold in the more open woods, but are absent from dense woods with a pure sand substratum. The leaf-mold, on the other hand, seems to be of chief importance to the true forest species, since they frequently occur in open woods with a thin layer of mold on the surface, but seldom in shady woods with a sand floor. Dense woods without leaf-mold are therefore very poor in species and individuals, while the most luxuriant herbaceous vegetation is developed in relatively open woods with a thin layer of mold.

The species of the prairie group persist within the edge of the forest, and are at first dominant. Farther back from the margin the prairie species may include both invaders from the bunch-grass

and relics of a former prairie occupation. It is always difficult and usually impossible to distinguish the two. It may be assumed that most of the annuals and the more abundant perennials with effective means of dispersal are invaders, while rare or solitary perennials are relics. *Aster sericeus* is one of the most reliable examples of this type. As the forest increases in density, the sun-loving prairie species become more and more restricted to the small openings between the trees (Pl. XIV, Fig. 2). There the number and character of the species vary very regularly with the size of the opening. For illustration, in the Oquawka area openings 12-15 ft. (4-5 m.) across usually contain *Opuntia Rafinesquii* and *Rudbeckia hirta*, while others of twice the diameter may have in addition *Panicum pseudopubescens*, *Carex Muhlenbergii*, and *Bouteloua hirsuta*. In general, the perennial members of the group extend farther into the shade, and the interstitial annuals are more intolerant; few species appear, and they are usually limited to the larger openings between the trees. This feature of distribution is probably correlated with the duration of life of the plants, and the demands of their seedlings for certain definite light conditions. Some species do not occur beyond the more open woods or the larger open spots. Such are *Petalostemum purpureum*, *Pentstemon hirsutus*, *Tradescantia reflexa*, *Lespedeza capitata*, *Lithospermum Gmelini*, *Viola pedata*, and many others. Some species grow well and reach a normal size in the sun, while in the shade they are stunted or sterile. Shade plants of *Coreopsis palmata* are weak and lax, with thin divaricately lobed leaves; *Physostegia denticulata* is weak and thin-leaved, contrasting sharply with the stout, thick-leaved form in full sun; *Tephrosia virginiana* grows with single stems instead of dense bunches; the bunch-grasses are loose and lax, and tend to lose their bunch habit. *Andropogon furcatus* and *A. scoparius* are more tolerant than the other bunch-grasses, but in the shade they lose their bunch habit completely, sending up single culms which have a few long spreading leaves and are always sterile. *Rudbeckia hirta* and *Poa pratensis* seem to have about the same light requirements. Both are found only in the more open woods or in sunny places, and are very frequently associated. Notwithstanding the limitations in their distribution, a few of these plants play an important part in the composition of the association, and are almost as characteristic of the forest as some members of the forest group proper. They are *Lithospermum Gmelini* and *Rudbeckia hirta*, because of their conspicuous showy flowers, *Tephrosia virginiana*, because of its bunch habit, and *Lespedeza capitata*, because of its great frequency and abundance. These four occur in every area of the association.

Seventy-one species may be regarded as typical of the forest rather than the prairie, and of these, nineteen represent pioneers in the succession of another, more mesophytic, type of forest, leaving fifty-two to characterize the black oak association.

The most distinctive feature of the flora is the large proportion of perennial herbs. Thirty-nine species, or 75 per cent. of the total, belong in this general group. Contrasted with the same group in the bunch-grass association, the chief difference is in the smaller number of bushy forms, a type which seems to belong primarily to the more xerophytic prairie formation. The bushy perennials of the oak forest are almost without exception more abundant in and more characteristic of the bunch-grass association. *Callirhoe triangulata* and *Asclepias tuberosa* send up several ascending stems from a common base; *Phlox bifida* is divergently branched and may assume a rounded shape; *Helianthemum majus* has erect stems which frequently grow in clusters. Nearly all of these plants live also in the bunch-grass association. By far the greatest number of species have erect, simple or sparingly branched stems, without a large number of basal leaves, growing singly or in small loose clusters. *Pteris aquilina* lives in large patches, spreading by its rhizomes, and *Pedicularis canadensis* has the same habit on a small scale. *Fragaria virginiana,* var. *illinoensis,* and *Potentilla canadensis* are also gregarious, spreading by runners. *Synthyris Bullii* has a basal rosette of large suborbicular leaves which are closely appressed to the ground.

A considerable number of species belonging to the interstitial group of the prairie associations live also in the forest, but are limited usually to sunny places or the more open woods. Only four characteristic species of the forest have this habit, and these plants are neither common nor widely distributed. They are *Anychia polygonoides,* in the Hanover, Havana, and Oquawka areas, *Castilleja coccinea,* in the Winnebago area, *Gnaphalium polycephalum,* in the Oquawka and Amboy areas, and *Krigia virginica* in the Havana area. From an ecological standpoint, this group is of very slight importance.

Shrubs are much more abundant in the forest than upon the prairie. *Rhus canadensis,* var. *illinoensis* is the most abundant and grows in irregular thickets, seldom exceeding two feet (5 dm.) in height, but from 3-30 ft. (1-10 m.) wide. It was not observed in the Winnebago or Amboy areas, where its place is taken by the equally abundant *Salix tristis* growing in thickets of the same general structure. *Ceanothus americanus* is found in all five areas and is locally abundant. *Rosa humilis* is common in the Hanover and Winnebago areas. *Rhus glabra* is occasional and a single individual of *Pyrus americana* was found in the Winnebago area.

One of the most noteworthy plants is a species of *Geaster,* which is abundant in each of the five areas, especially in open woods or near the edge of the forest.

Although the total number of species in the association is large, the number per unit of area is scarcely greater than in the prairie. Counts of a series of quadrats each two meters square, in the Winnebago area, showed an average of 6.5 species per quadrat. The forest there was rather open, with a thin deposit of mold, and the conditions for plant life near the optimum. In the whole field of about twenty acres (8 hectares) 32 species occurred. The number of species in the whole association is large, as might be expected in a type of such wide distribution and extent, but less than half of the total live in any one of the five areas examined. The small number in any individual station and the large number for each quadrat produce a monotonous uniformity throughout the association and prevent the recognition of definite consocies.

The following list gives the ecological grouping of the component species.

A. Species typical of the black oak association

1. Trees:

Quercus velutina
Quercus marilandica
Carya cordiformis

2. Perennial herbs:

Pteris aquilina
Smilacina stellata
Comandra umbellata
Fragaria virginiana, var. *illinoensis*
Potentilla arguta
Potentilla canadensis
Lupinus perennis
Desmodium illinoense
Euphorbia corollata
Callirhoe triangulata
Lechea sp.
Helianthemum majus
Zizia aurea
Asclepias tuberosa
Asclepias amplexicaulis
Asclepias verticillata
Physostegia denticulata
Scrophularia leporella
Pentstemon grandiflorus
Synthyris Bullii
Gerardia grandiflora
Pedicularis canadensis
Galium pilosum
Liatris scariosa
Solidago speciosa, var. *angustata*
Solidago nemoralis
Aster azureus
Rudbeckia hirta
Helianthus occidentalis
Helianthus strumosus
Artemisia caudata
Cacalia atriplicifolia

Apocynum androsaemifolium
Phlox bifida
Monarda fistulosa
Monarda mollis
Krigia amplexicaulis
Hieracium longipilum
Hieracium canadense

3. Shrubs:

Salix tristis
Rosa humilis
Pyrus americana
Rhus glabra
Rhus canadensis, var. *illinoensis*
Ceanothus americanus

4. Annuals and interstitials:

Anychia polygonoides
Castilleja coccinea
Gnaphalium polycephalum
Krigia virginica

B. Species more typical of the prairie associations

Andropogon furcatus
Andropogon scoparius
Sorghastrum nutans
Leptoloma cognatum
Paspalum setaceum
Panicum virgatum
Panicum perlongum
Panicum Scribnerianum
Panicum pseudopubescens
Stipa spartea
Aristida tuberculosa
Sporobolus cryptandrus
Calamovilfa longifolia
Koeleria cristata
Bouteloua hirsuta
Trideus flavus
Cyperus filiculmis
Carex pennsylvanica
Carex Muhlenbergii
Tradescantia reflexa
Commelina virginica
Rumex Acetosella
Polygonella articulata
Talinum rugospermum
Anemone cylindrica
Lepidium virginicum
Tephrosia virginiana
Lespedeza capitata
Strophostyles helvola
Polygala polygama
Crotonopsis linearis
Euphorbia Geyeri
Ceanothus americanus
Hudsonia tomentosa
Viola pedata
Opuntia Rafinesquii
Oenothera rhombipetala
Acerates viridiflora
Acerates viridiflora, var. *lanceolata*
Lithospermum Gmelini
Teucrium canadense
Scutellaria parvula
Monarda punctata
Physalis heterophylla
Physalis virginiana
Linaria canadensis
Pentstemon hirsutus
Ruellia ciliosa
Diodia teres
Specularia perfoliata
Liatris cylindracea

Arabis lyrata
Polanisia graveolens
Cristatella Jamesii
Cassia Chamaechrista
Baptisia bracteata
Amorpha canescens
Petalostemum candidum
Petalostemum purpureum
Aster sericeus
Aster linariifolius
Antennaria sp.
Ambrosia psilostachya
Coreopsis palmata
Artemisia caudata
Senecio Balsamitae

C. Forest species, typical of succeeding associations

Polygonatum commutatum
Smilacina racemosa
Smilax herbacea
Smilax ecirrhata
Smilax hispida
Populus grandidentata
Corylus americana
Silene stellata
Anemone virginiana
Ribes gracile
Rubus occidentalis
Prunus virginiana
Rhus Toxicodendron
Vitis vulpina
Psedera quinquefolia
Cornus Baileyi
*Monotropa uniflora**
Fraxinus pennsylvanica, var. *lanceolata*
Eupatorium serotinum
Prenanthes alba

D. Ubiquitous weeds and naturalized species

Poa pratensis
Poa compressa
Juncus tenuis
Chenopodium album
Saponaria officinalis
Oxalis corniculata
Oenothera biennis
Asclepias syriaca
Verbena stricta
Nepeta Cataria
Leonurus Cardiaca
Solanum carolinense
Solanum nigrum
Verbascum Thapsus
Erigeron ramosus
Achillea Millefolium
Lactuca canadensis

E. Species of doubtful position in the sand region

Rumex altissimus
Solidago serotina
Silphium integrifolium

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*Not observed in the bur oak association, but, from its general habit, probably more typical there.

SUCCESSIONS FROM THE BLACK OAK ASSOCIATION

In Illinois, succession between different types of forest is usually caused by the disturbance of some feature of the physical environment by physiographic changes. It therefore becomes possible to correlate the succession of forests with the physiography (Cowles, *1901*). In the sand areas of the state, however, physiographic processes are primarily not concerned, and the whole process is due to the reaction of the plant upon its habitat, by which there is developed a different habitat, adapted to a different type of vegetation. The chief feature of the vegetation by which these environmental changes are caused is the general density of the plant covering. This leads to the partial exclusion of sunlight, heat, and moisture from the soil, and to the addition every autumn of a large quantity of vegetable matter. In this way the soil moisture is conserved, the transpiration of the plants is diminished, and a layer of leaf-mold is slowly formed. The leaf-mold also aids in the conservation of moisture in the soil and at the same time increases its capacity for holding water. All of these changes go on simultaneously, and each is correlated with the others. The whole is in a mesophytic direction and, as a result, the xerophytic black oak association is succeeded by vegetation of a more mesophytic type, consisting of at least two, and possibly more, distinct associations. For the present, that of the Winnebago and Amboy areas will be considered as one, termed the bur oak association, and that of the Hanover, Havana, and Oquawka areas as another, the mixed forest association.

THE BUR OAK ASSOCIATION

In the Winnebago area the sand is distributed in irregular ridges, separated by irregular depressions of various sizes. The latter are occupied by an association characterized by bur oak, *Quercus macrocarpa*, and white oak, *Quercus alba*, together with a distinct type of herbaceous flora. None of the narrower upland ridges has as yet been succeeded by the bur oak association, although some show indications of it in the presence of scattered plants of choke-cherry, *Prunus virginiana*, black cherry, *Prunus serotina*, and hazel, *Corylus americana*. The bracken fern, *Pteris aquilina*, also becomes more abundant near the bur oak association (Pl. XV, Fig. 1), and its presence in large quantities may in some degree be considered as one indication of the approaching succession. On some ridges there is a well-defined zone of *Pteris* along the slopes, extending neither into the xerophytic black oak timber above, nor into the mesophytic bur

oak forest below. This type of distribution has been observed only on the narrower ridges, along the crests of which the xerophytic habitat is more emphasized and where the accumulation of humus takes place more slowly. On the broader uplands *Pteris* is usually common. Some of the latter show a transition to the bur oak type in the presence of *Pyrola elliptica, Amphicarpa Pitcheri, Vitis vulpina,* and *Agrimonia mollis,* typical members of the latter association. On the slopes from the black oak into the bur oak association there is usually a well-defined tension zone (Pl. XV, Fig. 2) where the plants of both groups mingle. Among these the most abundant are *Pteris aquilina* and *Smilacina stellata* of the black oak association and *Geranium maculatum* and *Prunus virginiana* of the bur oak.

The sharpness of the tension line, coupled with the slow development of the dominant species of the two associations, indicates a condition approaching an equilibrium between the two associations. Their common boundary on the steeper slopes seems to depend upon the water content of the sand as influenced by the height above the water-table, while on the broader uplands the incipient succession may depend not only upon the depth of the water-table, but to a greater extent upon the increase in water capacity through the development of humus. The present location of small ponds in the sand deposits shows that the actual depth of the water-table is several yards, and in all probability too great to explain the sharp tension line already noted. Its origin must accordingly be referred back to a past condition in which the general water-level was higher. Trees of *Quercus velutina* in the lower portions of the bur oak association are very few in number and usually small in size, showing that they are not relics, but recent sporadic invaders, and there is an unusually small number of herbaceous relics. In the upland portions of the bur oak association relic trees of black oak are numerous and frequently of large size, while many relic herbaceous species also occur. Throughout the black oak association pioneers of the bur oak group are well represented, as is shown by the list given in the discussion of the former association. All these peculiarities lead to a choice of two conclusions: the depressions have never been occupied by black oak, or the succession by the bur oak has been extraordinarily complete. Further evidence leading to the acceptance of the first alternative is afforded by conditions in the Amboy area and to some extent also in the Kankakee area.

In the Amboy area the sand lies in similar ridges mostly parallel to Green river and not over 60 feet (20 m.) above it. The inter-

vening valleys are for the most part filled with extensive deposits of muck overlying sand and occupied by swamp vegetation, with *Iris versicolor, Typha latifolia, Rhexia virginica, Houstonia coerulea, Populus tremuloides*, and other species of similar habitat preferences. Outside these depressions, and accordingly above them, lies the bur oak association, above which in turn is the black oak association, occupying the crests of the ridge. In every case the bur oak type is characteristic of the more mesophytic sand near the water-level. According to all established principles of succession the drainage of the intervening swamps would cause a downward migration of the bur oak association, provided other features of the environment were favorable to it. It is, of course, hardly probable that the bur oak would extend very far out upon the deposits of muck. If the swamps were composed of sand instead of muck, it is very probable that the whole area would be occupied by the bur oak association as rapidly as the lowering of the water-level permitted. In the Kankakee area the interdunal depressions are occupied by meadows, which are doubtless very similar to the Amboy swamps, having a number of species in common, and probably representing a further stage in the succession on muck or peat. The ridges are all covered with forest, but in the short trip made through the area the distinctions made between the black oak and bur oak associations were not recognized.

The whole leads to the first alternative mentioned, that the depressions in the Winnebago area have never been occupied by the black oak association, and that the bur oak association, which now occupies them, represents the present culmination of a past hydrophytic to mesophytic succession, which has been so far completed that scarcely a trace of it is now in existence.

This conclusion is supported by the presence of a single small pond occupying a depression in a partially cleared field. The few plants remaining indicate that the surrounding vegetation was of the bur oak type. The swamp vegetation at its margin is scanty, consisting of *Scirpus validus* and *Steironema lanceolatum*, outside of which are successive zones of *Populus tremuloides* and *Solidago graminifolia*. Further details were not noted.

The development of the muck soil in the depressions of the Amboy and Kankakee areas and its absence in those of the Winnebago area must also be explained. The latter areas are essentially fluviatile; their depressions are not far above the beds of the Green and the Kankakee rivers, respectively, and the lowering of the water-level is entirely dependent upon changes in the river level and upon deposi-

tion of soil. A slow change in the water-level, for such it must have been along these comparatively sluggish streams, would permit the long-continued existence of swamps and the consequent accumulation of large deposits of muck. In the Winnebago area, on the other hand, the deposits lie many feet above the Rock, Sugar, and Pecatonica rivers; swamps would be of short duration and the accumulation of muck would not take place. Consequently, the depressions have been occupied almost entirely with the bur oak association, with the exception of the single pond already mentioned. of the hydrophytic extreme is, as usual, chiefly due to changes in the water factor, while that of the xerophytic extreme is in this case

The development of the bur oak association represents, therefore, another case of the interpolation of a mesophytic mean association between a hydrophytic and a xerophytic extreme. The succession caused primarily by the development of humus. The whole probable successional history is indicated upon the diagram (Fig. 6.) showing the relation of the various associations.

The preceding statements concerning the development of the bur oak association following the swamp vegetation does not imply that it was the first type of forest to appear. On the other hand, there is some fragmentary evidence that an entirely different forest association preceded it.

Within the bur oak association (Pl. XVI, Fig. 1), *Quercus macrocarpa* is everywhere the prevailing tree. In the Amboy area, it was the only arborescent species in the small areas examined. In the Winnebago area it is mixed with white oak, *Quercus alba*, and shellbark hickory, *Carya ovata*. The former composes 25-50 per cent. of the whole, while there is seldom over 2 per cent. of hickory. The trees are larger and straighter than those in the black oak association, but still much inferior to those of their own species growing on a more fertile soil. A large number of shrubs form a second layer beneath them, and are often aggregated into dense thickets. *Prunus serotina*, *Prunus virginiana*, and *Corylus americana* are by far the most abundant, with several other occasional species. Lianes are not common, and consist of scattered individuals of *Vitis vulpina*, *Smilax hispida*, and *Rhus Toxicodendron*, with a few other species of less importance.

The forest cover is dense and the light diffuse. This prevents the growth of most grasses, except where the forest has been partially cleared. The ground cover is composed chiefly of a dense luxuriant growth of herbaceous plants. They are of a larger average size and much more mesophytic appearance than those of the black oak ridges.

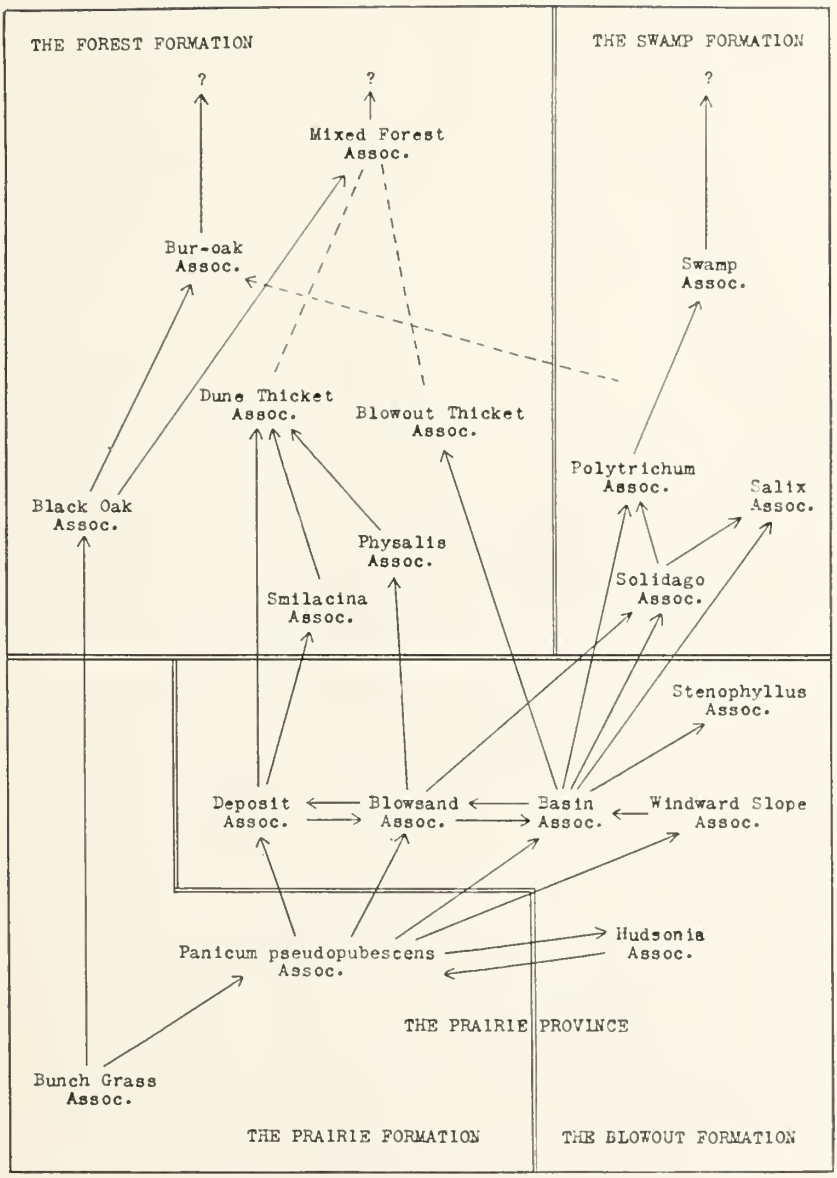

Fig. 6. Diagram showing the plant associations of the inland sand deposits of Illinois, and the principal successions between them.

Although comparatively few in number, their distribution is remarkably uniform, so that the various areas occupied by the association are strikingly similar in their vegetational appearance. On the uplands, it is more or less mixed with relics of the preceding black oak association.

An association greatly resembling this, and possibly identical with it, occupies in the Winnebago area the upland areas of clay overlying limestone, and indicates that, in the future development of the vegetation, the associations on sand and clay will become gradually similar. This is in accordance with the views of Cowles (*1901: 7*), that all the vegetation of a region "is tending toward an ultimate common destiny."

The specific composition of the association is shown by the following list.

A. Species characteristic of the association

1. Trees:

Quercus macrocarpa
Quercus alba
Carya ovata

2. Smaller trees and shrubs:

Populus tremuloides
Populus grandidentata
Corylus americana
Rubus idaeus, var. *aculeatissimus*
Rubus occidentalis
Prunus serotina
Prunus virginiana
Cornus Baileyi

3. Lianes:

Smilax herbacea
Smilax ecirrhata
Smilax hispida
Rhus Toxicodendron
Vitis vulpina
Psedera quinquefolia
Lonicera Sullivantii

4. Herbs:

Botrychium ternatum, var. *intermedium*
Botrychium virginianum
Polygonatum commutatum
Smilacina racemosa
Cypripedium parviflorum, var. *pubescens*
Silene stellata
Arenaria lateriflora
Heuchera hispida
Agrimonia mollis
Desmodium grandiflorum
Amphicarpa Pitcheri
Geranium maculatum
Circaea lutetiana
Sanicula canadensis
Pyrola elliptica
Dodecatheon Meadia
Veronica virginica
Galium concinnum
Prenanthes alba

B. Species more typical of preceding associations

Pteris aquilina
Poa pratensis
Tradescantia reflexa
Salix tristis
Quercus velutina
Fragaria virginiana, var. *illinoensis*
Rosa humilis
Amorpha canescens
Euphorbia corollata
Ceanothus americanus
Apocynum androsaemifolium
Monarda mollis
Synthyris Bullii
Gerardia grandiflora
Pedicularis canadensis
Antennaria sp.
Helianthus strumosus
Coreopsis palmata
Cacalia atriplicifolia

THE MIXED FOREST ASSOCIATION

In the Hanover, Oquawka, and Havana areas the succession from the black oak association is dependent primarily upon a general and gradual increase in the water content of the sand and a corresponding decrease in the light, without the concurrence of historical factors as in the two areas previously described. The succeeding vegetation is derived wholly from the surrounding associations. Since other types of vegetation are developed best near the rivers which border these sand areas, invasion begins near the river and gradually extends back toward the center of the sand deposits, so that the most advanced stages in the succession are always found near the river. The development of this succession is greatest in the Havana and least in the Hanover area; a feature which is perhaps correlated with the general southeastern origin of the forest formation.

In the Havana area, as in the Winnebago deposits, the narrower ridges of sand are the last to be affected by this succession, while the broader ridges or those near the river generally show some indication of it. Certain species are soon recognized as the normal pioneers in the succession, and while their order of appearance is not constant, their presence is always connected with the development of a thin, fibrous layer of leaf-mold over the surface of the sand. It is frequently possible to observe nearly all stages in the succession in a distance of a mile, passing from the edge of the forest toward its center. In some places, adjacent ridges of sand represent different stages of the succession, and permit an easy comparison of the vegetation. This is especially well shown on the first two forested ridges east of Havana, about two miles (3 km.) from that city. The first of these represents an advanced stage of the succession, while the second is occupied by a nearly typical black oak association.

Excluding the two species of oaks, the ridges have 29 and 31 species, respectively, of which only ten are common to both. This gives a community coefficient (Jaccard *1902:* 351) of 0.200, indicating at once the great floral dissimilarity. There are, on the other hand, thousands of acres still occupied by the black oak association, with as yet no indication of the approaching succession.

Rhus canadensis, var. *illinoensis, Tephrosia virginiana,* and *Opuntia Rafinesquii* are the chief species concerned in accumulating fallen leaves for conversion into leaf-mold. With the simultaneous decrease in light, the succession begins, and occasional plants of *Polygonatum commutatum* and *Silene stellata* appear as pioneers. *Agrimonia mollis* comes in somewhat later, and young plants of three lianes appear. These are *Vitis vulpina, Rhus Toxicodendron,* and *Psedera quinquefolia.* The last is especially common and valuable as a succession index. Its long, slender stems trail for several feet along the ground, unless by chance they encounter a tree trunk to climb. *Rhus Toxicodendron* seldom trails, but usually grows directly at the base of some tree. Following these six species, which are easily recognized as pioneers, a number of others appear in irregular order. The arborescent flora remains essentially the same, except for occasional trees of *Celtis occidentalis* or *Prunus serotina,* or, near the river, *Quercus rubra, Quercus macrocarpa, Juglans nigra, Ulmus americana, Morus rubra,* and *Gymnocladus dioica.* The undergrowth is frequently dense, with numerous thickets of shrubs, and the herbaceous growth is tall and luxuriant. The following additional species are especially characteristic:

Asparagus officinalis
Smilacina racemosa
Smilax herbacea
Dioscorea villosa
Anemone virginiana
Ribes gracile
Celastrus scandens
Oenothera biennis
Sanicula canadensis
Cornus Baileyi
Asclepias phytolaccoides
Lappula virginiana
Scrophularia leporella
Galium concinnum
Eupatorium purpureum
Eupatorium urticaefolium

It will be noted that a majority of these species have unusually efficient means of seed dispersal. When an association develops *de novo* some distance from the nearest existing area of it, the most mobile species may naturally be expected to appear first, while the less mobile species follow after greater intervals of time. The species in the preceding list accordingly represent the mobile pioneers of an association, the usual dominant species of which have as yet not ap-

peared. Near the Illinois river there are some rather extensive sand fields occupied by a forest characterized particularly by bur oak and white oak, with several other arborescent species, such as red oak, *Quercus rubra,* elm, *Ulmus americana,* hackberry, *Celtis occidentalis,* and white ash, *Fraxinus americana.* This probably represents the complete succession, the beginning of which has been indicated above. Intermediate stages, however, have not been observed.

In the Oquawka area the succession is found only on the long dunes nearest the river. The first indication of it is given by *Silene stellata, Polygonatum commutatum,* and *Psedera quinquefolia,* which are followed by a number of additional species, including several trees. The whole leads to the highest type of mesophytic forest (Pl. XX, Fig. 2, background) that occurs on the sand deposits.

The succession is best seen along the dune nearest the river, north of the town of Oquawka, and may be traced through various stages from north to south for a distance of about 1.5 miles (2 km.). This dune has a maximum height of about 100 feet (30 m.), indicating a very strong and continued wind action at some time in the past. It is now completely covered with trees, and the surface layers of sand are well mixed with organic matter. At the north end a bayou of the Mississippi lies at its base, and the margin of the water is marked by a line of elms and willows, with *Rumex verticillatus, Physostegia virginiana,* and other species of hydrophytic tendencies. *Equisetum hyemale* is the only one of these which extends much above the water-level, where it mingles with the usual sand-dune species. Along the north end of this ridge the prevailing trees are *Quercus velutina* and *Quercus marilandica,* with occasional trees of *Quercus rubra,* especially on the lower part of the slope. Besides the pioneer herbaceous species mentioned above, there are also *Strophostyles helvola, Monarda fistulosa, Aquilegia canadensis,* and *Vitis vulpina.* Somewhat farther toward the south *Juglans nigra* appears near the base of the hill not far above water-level; farther along it extends higher and even appears at the top of the dune. *Cercis canadensis* is usually found with it. In the same way the river birch, *Betula nigra,* the elm, *Ulmus americana,* the green ash, *Fraxinus pennsylvanica,* var. *lanceolata,* and finally the soft maple, *Acer saccharinum,* appear first at the bottom of the dune and as mesophytic conditions increase toward the southward extend higher and higher above water-level, until they finally appear at the top. Each one of these species is more moisture-loving than its predecessors, until the climax is reached in the soft maple, a characteristic tree of river-bottom swamps, here growing many feet above the water.

The change in the herbaceous and shrubby flora and ground cover is no less manifest. *Cornus Baileyi* and *Scrophularia leporella* soon appear; *Celastrus scandens* becomes a common liane; and *Zanthoxylum americanum* grows high above the river. Following these, dense mats of moss and *Peltigera* cover the sand and aid in the increase and conservation of soil moisture. With them come such pronounced mesophytes as *Parietaria pennsylvanica, Aster oblongifolius, Anychia canadensis,* and finally *Woodsia obtusa* and *Anemone canadensis.* The last species, together with the soft maple, is sufficient proof of the extraordinary change that has taken place in the water factor. Bare sand is seldom exposed, but is covered with the dense mats of moss and *Peltigera,* and shaded by the luxuriant tangle of herbaceous plants and shrubs. The few bare spots are still occupied with the typical black oak vegetation of *Artemisia caudata, Rudbeckia hirta,* and other similar species.

The further fate of this association will be described later in connection with the vegetational history of the river dune as a physiographic form.

In the Hanover area, the conditions which lead to succession are virtually the same as in the Havana area, but a much smaller area has been affected. *Psedera quinquefolia* is one of the pioneers, as usual, and is followed by a considerable number of species of mesophytic character. Among these are the following.

Trees:

Betula nigra
Ulmus americana
Celtis occidentalis
Fraxinus pennsylvanica, var. *lanceolata*

Shrubs:

Ribes gracile
Rubus idaeus, var. *aculeatissimus*
Rubus occidentalis
Prunus virginiana
Rhus glabra
Ceanothus americanus
Cornus Baileyi

Lianes:

Smilax cirrhata
Smilax herbacea
Menispermum canadense
Rhus Toxicodendron
Vitis vulpina

Herbs:

Polygonatum commutatum
Silene stellata
Amphicarpa Pitcheri
Ziza aurea

Aquilegia canadensis
Ranunculus abortivus
Heuchera hispida
Fragaria virginiana,
var. *illinoensis*
Geum canadense
Asclepias phytolaccoides
Apocynum androsaemifolium
Monarda mollis
Eupatorium serotinum
Eupatorium urticaefolium
Antennaria plantaginifolia

The River Dunes and their Plant Associations

In the preceding pages those various associations have been described which comprise most of the vegetation of the sand areas. The chief physical factors concerned in molding their topography or differentiating their associations have been wind and soil moisture. There remains to be discussed the narrow strip of dunes which lies close along the Mississippi river and which is affected also by water action. The river dunes are well developed in the Hanover and Oquawka areas along the Mississippi river, whose swift current and shifting channel have been chiefly responsible for their origin. They are much less prominent along the Illinois river, whose sluggish current possesses but little power of erosion. The first stages in the vegetational history of the dunes were observed only in the Hanover area; the last, from and including the development of the oak forest, only in the Oquawka area.

In the first two areas, the sand deposits lie at an average height of 15-30 feet (5-10 m.) above the swampy, alluvial flood-plain. The river meanders across its flood-plain from side to side, and in some places flows directly at the foot of a sand hill. Under these conditions a river dune may be formed. Erosion by the river carries away the sand from below, and that portion of the sand above the high-water mark of the river, and consequently removed from the direct erosive action, stands at a steep slope, the angle of which depends upon the wind, the rate of erosion, and the vegetative covering. The surface sand on this slope is exposed to the full sun and keeps loose and dry. Below ordinary high-water mark the sand is worked over by the water and lies at a gentle slope, forming a broad or narrow beach. The wind, which is generally from the west, removes sand from the lower slope, and to a less extent also from the steeper portion, carries it up the slope, and piles it in a long dune parallel with the river and several feet higher than the general level of the sand. As long as the river continues erosion on that part of its banks, the whole slope moves gradually back; if the wind constructs the dune as rapidly, or more rapidly, than the river erodes

it, the whole complex migrates slowly landward. If the river erodes more rapidly than the wind piles up the sand, the dune will soon be destroyed and only a bare slope remain. On the other hand, if the river shifts its channel, or for some other reason ceases erosion, the whole exposed surface will ultimately be fixed with vegetation and become static. From a physiographical standpoint, therefore, the whole dune consists typically of two divisions (Pl. XVII, Fig. 2): the lower, termed the middle slope, consists of sand now being uncovered and removed by the wind and erosion; and the upper, called the upper slope, of sand deposited by the wind, and removed by undermining through erosion. From the standpoint of vegetation, several associations may be distinguished which are in part correlated with the physiography.

The lowest portion of the dune, near the river and within reach of high water, is marked by vegetation of a semi-hydrophytic nature. When visited in June, 1908, the river was very high, and only the tops of the half-submerged plants could be seen. These were *Populus deltoides, Salix longifolia, Fraxinus pennsylvanica,* var. *lanceolata, Gleditsia triacanthos,* and *Ulmus americana,* typical sand-bar or river-bottom plants. The herbaceous vegetation of a later season is doubtless of the same ecological nature, probably including *Eupatorium serotinum, Xanthium commune,* and other species of similar habitat. This vegetation has no relation to the typical dune vegetation above it, except in the presence of a few individuals of *Panicum virgatum,* which had probably slid down from the slope above.

The vegetation of the middle slope clearly belongs to the blow-sand association, as described under the blowout formation. The plant covering is sparse, becoming somewhat dense toward the bottom. It consists chiefly of *Cassia Chamaechrista* and *Diodia teres,* with smaller numbers of *Croton glandulosus,* var. *septentrionalis, Ambrosia psilostachya,* and *Cristatella Jamesii.* At wide intervals are tufts of perennials, including *Accrates viridiflora,* var. *lanceolata, Panicum virgatum, Lithospermum Gmelini, Euphorbia corollata, Cyperus Schweinitzii,* and *Tephrosia virginiana.* The surface of the sand is dotted with numerous pebbles, sometimes as much as 2 inches in diameter. They apparently do not affect the vegetation, and there are not enough of them to be called gravel. They evidently represent the accumulation of pebbles left by the sand blowing up into the deposits above.

The top of the middle slope is marked by the outcrop of a layer of loamy sand (Pl. XVII, Fig. 2), very dark brown in color, rather fine-grained, and conspicuously earthy in texture. The top of this layer is well marked, but it gradually passes below into the typical orange-

brown sand of the middle slope. It is caused by past generations of plants which occupied this surface before the dune was formed, or at least before it had migrated so far inland. Since this soil blows, weathers, or dries out less rapidly or easily than the pure sand, the outcrop is marked by a slightly steeper slope and by dark-colored patches. Digging behind shows that the stratum extends indefinitely beneath the sand. For long distances the outcrop line is very distinct, but not perfectly level. Its elevation varies gradually, but irregularly, and in some places the whole outcrop disappears, corresponding to irregularities in the original level of the sand, or to locations of former blowouts. This soil stratum is on the same level as the country behind the dune and illustrates plainly the continued inward migration of the dune. (Cf. also Pl. XVIII, Fig. 2.) It is characterized now by a line of *Elymus canadensis*.

The upper slope consists of fine sand piled at an average angle of about 20 degrees. The vegetation is much like that of the middle slope, but denser and with many additional species (Pl. XVII, Fig. 2). It is likewise referred to the blowsand association. *Cassia Chamaecrista* and *Diodia teres* are again the most abundant species, and *Aristida tuberculosa* is also conspicuous. Other less characteristic species are *Monarda punctata, Lithospermum Gmelini, Euphorbia corollata, Diodia teres, Cristatella Jamesii, Ambrosia psilostachya, Oenothera rhombipetala, Linaria canadensis, Kuhnia eupatoriodes*, var. *corymbulosa, Acerates viridiflora*, var. *lanceolata* and var. *linearis, Oxybaphus nyctagineus, Teucrium occidentale, Tradescantia reflexa, Lespedeza capitata*, and *Rumex Acetosella*. In somewhat sheltered places *Scrophularia leporella, Draba caroliniana*, and *Corydalis micrantha* occur.

In some places, near the top of the slope, adjacent to the thickets described later, are associations of *Physalis heterophylla* (Pl. XVIII, Fig. 1). The individual plants grow in large patches and are very loosely aggregated, with a large amount of open sand between them, yet the patches are remarkably free from other plants. Even *Cassia* and *Diodia*, so abundant on the upper slope, are almost entirely absent from these patches. This peculiarity of distribution leads to the inference that they are more closely related ecologically to the thickets which crown the dunes than to the slope below. They may bear the same relation to the blowsand association that *Smilacina stellata* on the lee slope bears to the deposit association.

The crest of the river dune is primarily an area of deposit, and is consequently occupied at first by the regular deposit association, already described in connection with the blowout formation. *Rhus*

canadensis, var. *illinoensis* is again the most important member of the association. The perpetuation and vertical growth of the river dune are chiefly due to its efficiency as a sand-binder. The general height of the dune thus held is from 15-30 feet (5-10 m.) above the general level of the sand, but a maximum height of about 80 feet (25 m.) is attained in the Oquawka area, or fully 100 feet (30 m.) above the high-water level of the river. It is noteworthy that this highest point is occupied by a loose patch of *Rhus,* evidently of great age. Associated with *Rhus* on these dunes are similar dense patches of *Ceanothus ovatus* and, occasionally, of *Rhus Toxicodendron.* This shrubby habit of the last species was not observed elsewhere in the region, but is very common along the dunes of Lake Michigan, particularly toward the north, and is reported from Lake Erie by Jennings (*1909*). There are also the usual bunches of *Tephrosia virginiana, Panicum virgatum* (Pl. XX, Fig. 1), and, more rarely, *Eragrostis trichodes* and *Sporobolus cryptandrus.* Intervening spaces of open sand are occupied by the usual members of the blowsand association.

If the erosion by the river proceeds at such a rate that the crest of the dunes remains relatively stable for some years, opportunity is given for the development of a higher type of vegetation. The first step in this succession depends upon the introduction of seeds by wind or animals from the alluvial bottom-lands. The species most frequently introduced in this way are *Ulmus americana* and *Fraxinus pennsylvanica,* var. *lanceolata,* both of which have light winged seeds. Pods of *Gleditsia triacanthos* are blown up the slope from the trees on the river bank below, and more rarely *Juglans nigra* develops from seeds probably carried by animals. Seeds of *Acer saccharinum* were also found on the dunes, but they probably do not germinate, since no young plants were seen. These trees are not numerous, and never reach a large size, partly because of the unfavorable habitat, but chiefly because of the general movement of the dune. All the older trees have portions of their root systems exposed. One ash tree, 8 inches (2 dm.) in diameter, had the base of its stem 3 feet (1 m.) above the surface and 15 feet (5 m.) behind the present crest of the dunes (Pl. XVIII, Fig. 2). The ash, which is by far the most abundant of the trees, usually branches freely from the base, forming a complex of stems.

The trees offer a roosting place for birds, which in turn serve as agents in the dispersal of several shrubs and lianes. These at once spring up beneath the trees, and develop the dune thicket association. The mature thickets (Pl. XIX, Fig. 1) are exceedingly dense, impenetrable tangles of shrubs and lianes, with an occasional tree, half

smothered with vines, rising above them. Eight species of shrubs or small trees and seven species of lianes are concerned and, with a single exception, all have seeds adapted to dispersal by birds. They are as follows:

Smilax herbacea
Smilax hispida
Salix longifolia
Celtis occidentalis
Menispermum canadense
Ribes gracile
Pyrus ioensis
Prunus virginiana
Prunus serotina
Prunus sp. (plum)
Rhus Toxicodendron
Celastrus scandens
Psedera quinquefolia
Vitis vulpina
Cornus Baileyi

The choke-cherry (*P. virginiana*), plum, and crab (*Pyrus ioensis*) are the most abundant shrubs. The plum has running roots which send out shoots at short intervals, so that it tends to spread out upon the blowsand. The lianes are usually luxuriant and cover the shrubs with such masses that the supports are almost hidden. Within the thicket the light is very low; many of the branches are leafless or dead, and the herbaceous vegetation is scanty. It consists of *Teucrium occidentale*, *Scrophularia leporella*, *Polygonatum commutatum*, and *Smilacina racemosa*, with seedlings of *Psedera quinquefolia*. These thickets occupy the crest of the dunes and usually extend also some distance down the lee side. In some places the advance of the dune is sufficiently rapid to bring a portion of the thickets over to the windward side, where they are soon undermined (Pl. XIX, Fig. 2).

The further fate of these thickets is not known. It is worthy of note that they are somewhat similar in floristic composition to the thickets developing in certain blowouts, as described elsewhere in this paper (p. 107) and also in an earlier article (Hart and Gleason, *1907:* 168). Many of the species concerned are also characteristic of the mixed forest association and indicate a possible succession in that direction.

Just at the margin of the thickets on the lee side, and partially shaded by them, patches of *Smilacina stellata* frequently occur. The plant spreads by running rootstocks, but is not efficient as a sand-binder. The few patches on the windward side of the thickets are very soon undermined and destroyed. This small association encroaches upon the deposit association in advance of the thickets, and is dependent upon the thickets for a partial protection from sunlight. It illustrates a peculiar case of succession in which an early stage is dependent upon a later stage for its existence and appears only after

the later stage (in this case the dune thicket association) is well developed.

Blowouts may be formed on the crest of the river dune in the usual way, and extend transversely through it. They seldom reach below the old soil bed which marks the limits of the middle slope. Their vegetation is of the usual type, except that the lateral slopes are frequently held by the plums and crabs of the thicket association.

In some places in the Hanover area the river dune is occupied by the black oak association. The erosion there is generally feeble and the dune relatively stable. It seems probable that the oaks would also develop on the dunes stabilized by the ordinary deposit association if the thickets did not encroach upon them so rapidly. *Smilacina stellata,* as already mentioned, is a characteristic member of the black oak association, and its position on the dunes between the thicket and the deposit associations possibly indicates a potential development of the black oak forest at this place.

In the Oquawka area the greater portion of the river dune is forested, and in parts of it the development of humus and the increased density of the ground cover has led to the establishment of a mesophytic type of forest, described already (p. 137) under the mixed forest association. This portion of the dune is no longer washed by the river itself, but by some sluggish bayous representing a former channel of the river and separated from the present channel by a number of densely wooded alluvial islands. At the foot of these islands the channel bends eastward against the foot of the dune and erosion is now proceeding rapidly. The plant covering is an efficient protection against wind erosion, and the dune would be completely stable if it was farther inland, but it can not resist the undermining effect of the water. On a strip several hundred yards long the forest has been completely destroyed (Pl. XX, Fig. 1), and the vegetation now consists entirely of the blowsand and deposit associations. At the north end of the deforested portion the destruction of the forest is still proceeding. The effect of the erosion is first manifested at the foot of the dune, and its influence gradually extends higher until eventually the trees at the top are undermined. There is thus produced a triangular extension of the blowsand, extending like a wedge along the river between the water below and the forest above. It is now seen that the principal root development of the herbaceous vegetation extends but one or two feet (3-5 dm.) below the surface, and binds the sand into a coherent stratum resting on the loose sand beneath (Pl. XX, Fig. 2). The loose sand rests at as steep an angle as possible, and irregular blocks of the surface layer become detached

and slide slowly down the incline toward the river. Their sides are nearly vertical, and by their detachment the margin of the remaining forest association is left as a prominent vertical wall of coherent sand. The motion of these detached blocks is of course very slow; but that they are loose is at once demonstrated by stepping on one, which then immediately starts down the slope and in a short time comes to rest on the flat beach at the base of the dune. Their plant population is a relic of the former mesophytic vegetation, and consists largely of perennials with a root system extensive enough to bind the mass together. Some of the commoner species are *Lespedeza capitata, Tradescantia reflexa, Monarda mollis, Solidago nemoralis,* and *Artemisia caudata.* The more pronounced mesophytes of course disappear with the removal of the protecting trees.

The general trend of vegetation on the river dunes is therefore always toward stabilization, but their permanence is never certain because of the constant changes in the channel of the river. With the destruction of the higher types of vegetation by erosion, the pioneer blowsand association reappears and the successional cycle begins anew.

The Perched Dunes

In the Hanover area wind-blown sand has collected on top of the high bluffs which border the sand areas, and forms miniature dunes and blowouts. A number of typical sand plants have colonized upon them, and are usually accompanied by the more resistant species of the uplands or of the rocky hillsides. In the blowouts, which are always small, the vegetation represents the blowsand association and consists of *Scutellaria parvula, Linaria canadensis, Monarda punctata, Verbena bracteosa, Ambrosia psilostachya, Festuca octoflora,* and *Hedeoma hispida.* On the stabilized dunes there are also *Opuntia Rafinesquii, Artemisia caudata, Amorpha canescens, Lithospermum Gmelini, Rhus canadensis,* var. *illinoensis, Panicum pseudopubescens, Viola pedata,* and *Lespedeza capitata.* In the sandy soil under the oaks are *Cacalia atriplicifolia, Hypoxis hirsuta, Lithospermum Gmelini, Phlox pilosa, Antennaria* sp., *Anemone patens,* var. *Wolfgangiana, Erigeron pulchellus, Poa pratensis, Corylus americana,* and *Juniperus virginiana.*

Annotated List of Species

No attempt was made to secure a complete collection or a complete list of the plants living in the sand regions, and the list given

here could be greatly extended by further observation. Only the seed-plants, ferns, and fern-allies are included, and the usual habitat of each species is given by associations. Many unusual locations of species are omitted. The nomenclature follows the Vienna Code, as exemplified in the seventh edition of Gray's Manual.

Polypodiaceae

Pteris aquilina L. Winnebago, Amboy, and Havana areas, in the black oak association; Kankakee area, very abundant in the black oak forest and the intervening marshy meadows; sometimes persisting as a relic in the bur oak association in the Winnebago area.

Woodsia obtusa (Spreng.) Torr. Oquawka area, in the mixed forest association, growing in dense shade on mats of moss on the mesophytic portions of the river dune. Not observed elsewhere in the sand region.

Ophioglossaceae

Botrychium ternatum (Thunb.) Sw., var. *intermedium* D. C. Eaton. Winnebago area, in the upland portions of the bur oak association.

Botrychium virginianum (L.) Sw. With the last species.

Equisetaceae

Equisetum arvense L. Dixon area, in the *Solidago* association in extinct blowouts.

Equisetum hyemale L. Oquawka area, an invader from the alluvial flood-plain vegetation into the mixed forest association on the river dune.

Equisetum hyemale L., var. *intermedium* A. A. Eaton. Hanover, Dixon, and Havana areas, usually in the bunch-grass association; sometimes growing in dense masses and aiding in the stabilization of blowout deposits; abundant in the *Solidago* association in the Havana area.

Selaginellaceae

Selaginella rupestris (L.) Spring. Hanover area, in the bunch-grass association. It is frequently concerned in the fixation of sand and the re-establishment of the bunch-grass, and sometimes appears in the windward slope association of the blowouts. The growth rings formed by this plant have been described in the text.

Pinaceae

Juniperus virginiana L. Hanover area, frequent on the rocky exposed bluffs and from them invading the perched dunes.

Gramineae

Andropogon scoparius Michx. One of the most typical sand grasses in the Hanover, Amboy, Dixon, Oquawka, and Havana areas; very frequent in the bunch-grass association and persisting from it as a relic in the *Panicum pseudopubescens* and the black oak associations.

Andropogon furcatus Muhl. An abundant and important grass, but by no means as common as the preceding species. Hanover, Amboy, Dixon, Oquawka, and Havana areas, normally in the bunch-grass association, but persisting as a relic in the black oak and *Solidago* associations, and sometimes appearing on blowout deposits.

Sorghastrum nutans (L.) Nash. Hanover, Amboy, Oquawka, and Havana areas, in the bunch-grass association, and as a relic in the edge of the black oak association.

Digitaria filiformis (L.) Koeler. Hanover, Oquawka, and Havana areas, apparently not native, but coming in as a weed along roadsides or in too closely cropped pastures.

Leptoloma cognatum (Schultes) Chase. Abundant in each area except Winnebago and Kankakee, chiefly in the bunch-grass, where it may be dominant, also as a relic in the edge of the black oak association, in the *Panicum pseudopubescens* association, and on the windward slope of blowouts; it also appears early on blowout deposits.

Paspalum setaceum Michx. Hanover, Dixon, Oquawka, and Havana areas, typically in the blowsand association, and continuing on the deposits, also as an interstitial in the bunch-grass and in bare spots at the edge of the black oak association.

Panicum pseudopubescens Nash. Abundant in each of the five areas in a variety of situations; common in the bunch-grass association but usually as a secondary species; characteristic of the association to which it gives its name; persisting as a relic in the blowout succession in the windward slope and deposit associations; frequent in open sunny places in the black oak forest; rare in the blowsand association; and, in the Dixon area, depauperate plants persist in the mats of *Polytrichum*.

Panicum virgatum L. Common throughout but not abundant, usually in the bunch-grass association, but in the Hanover area one of the commonest dune-formers on the blowout deposits or the crest

of the river dunes; rare in open places in the black oak association, or as a relic in other situations.

Panicum perlongum Nash. Hanover, Havana, and Winnebago areas, common in the bunch-grass and *Panicum pseudopubescens* associations, or in open places in the black oak association.

Panicum Scribnerianum Nash. Only in the most mesophytic stations of the bunch-grass association in the Havana, Hanover, Dixon, and Oquawka areas; along roadsides and at the edge of the black oak forest in the Amboy and Winnebago areas.

Setaria glauca (L.) Beauv. Naturalized from Europe. Hanover area, a weed in pastured bunch-grass.

Cenchrus carolinianus Walt. Hanover, Dixon, Havana, and Oquawka areas; regularly in the blowsand association or as an interstitial on blowout deposits.

Stipa spartea Trin. In the bunch-grass association in the Hanover, Dixon, Havana, and Oquawka areas, more rarely on deposits or at the edge of black oak woods; also in a pastured field in the Winnebago area.

Aristida basiramea Engelm. Oquawka area, according to Patterson.

Aristida tuberculosa Nutt. Hanover, Dixon, Havana, and Oquawka areas, common as an interstitial in the bunch-grass and *Panicum pseudopubescens* associations, very abundant and characteristic in the blowsand association, common at the edge of the black oak forest, and in the Dixon area abundant in the *Solidago* association.

Sporobolus cryptandrus (Torr.) Gray. Chiefly in the blowsand and deposit associations of the Hanover, Havana, and Oquawka areas, sometimes in bare sunny spots in the black oak forest.

Sporobolus heterolepis Gray. Oquawka area, according to Patterson.

Calamovilfa longifolia (Hook.) Hack. Dixon, Havana, and Oquawka areas, in the bunch-grass association or persisting as a relic in open places in the black oak association.

Koeleria cristata (L.) Pers. Hanover, Winnebago, Dixon, and Oquawka areas, abundant and conspicuous in the bunch-grass; persisting as a relic in the black oak and *Panicum pseudopubescens* associations; and in rare cases appearing on blowout deposits.

Spartina Michauxiana Hitchc. Amboy area, along roadsides, doubtless adventive from the swampy meadows below.

Bouteloua hirsuta Lag. Hanover, Havana, and Oquawka areas, common but inconspicuous in the bunch-grass, where it grows as an

interstitial between the larger grasses, rarely persisting in the *Panicum pseudopubescens* and black oak associations.

Bouteloua oligostachya (Nutt.) Torr. Hanover area, according to Pepoon.

Bouteloua curtipendula (Michx.) Torr. Havana and Oquawka areas, in the bunch-grass association.

Tridens flavus (L.) Hitchc. Havana area, chiefly in the bunch-grass, but also in the black oak association and rarely as a relic in the *Panicum pseudopubescens* association.

Triplasis purpurea (Walt.) Chapm. Oquawka area, in the blowsand association, according to Patterson.

Eragrostis trichodes (Nutt.) Nash. Havana and Oquawka areas, typically in the bunch-grass but also in the black oak and deposit associations.

Eragrostis pectinacea (Michx.) Steud. Hanover, Havana, and Oquawka areas, always in the bunch-grass association.

Poa compressa L. Sunny places in the black oak association, Havana area.

Poa pratensis L. In a large variety of situations in each area, but chiefly where the land has been pastured or along roadsides.

Festuca octoflora Walt. Hanover, Winnebago, and Oquawka areas, chiefly as an interstitial in the bunch-grass, but also common in the blowsand association.

Hordeum pusillum Nutt. A weed along the roadsides in the Oquawka area.

Elymus virginicus L. Oquawka area, occasional in the bunch-grass association.

Elymus canadensis L. Hanover and Oquawka areas, in the bunch-grass association and sometimes as a relic in the *Panicum pseudopubescens* association.

Elymus striatus Willd. Oquawka area, a typically mesophytic species of the mixed forest association on the river dune.

Cyperaceae

Cyperus rivularis Kunth. Havana area, in the swamp association of an extinct blowout.

Cyperus Schweinitzii Torr. Hanover, Dixon, Havana, and Oquawka areas, chiefly in the bunch-grass; common also in the *Panicum pseudopubescens* association and rarely in the blowsand.

Cyperus filiculmis Vahl. Hanover, Winnebago, Havana, and Oquawka areas, a common interstitial of the bunch-grass, frequent

in the blowsand and *Panicum pseudopubescens* associations, and more rarely in open places in the black oak woods.

Eleocharis obtusa (Willd.) Schultes. In the swamp association in the Dixon and Havana areas.

Stenophyllus capillaris (L.) Britton. The characteristic species of the *Stenophyllus* association in the bottoms of partially stabilized blowouts in the Hanover, Havana, and Oquawka areas, rarely in the *Solidago* and bunch-grass associations.

Scirpus validus Vahl. Around the margin of a pond in a depression between the dunes, Winnebago area.

Scirpus cyperinus (L.) Kunth. Common in the swamp association and occasional in the *Salix* association in the Dixon area.

Carex festucacea Schkuhr, var. *brevior* (Dewey) Fernald. An interstitial in the bunch-grass association in the Hanover and Oquawka areas; not common.

Carex Muhlenbergii Schkuhr. Abundant in the bunch-grass association in the Hanover, Havana, Dixon, and Oquawka areas, and sometimes becoming the dominant species; one of the commoner bunch-grass relics in the *Panicum pseudopubescens* association; infrequent on the deposits and windward slopes of blowouts; in the black oak association in the Hanover, Winnebago, Havana, and Oquawka areas.

Carex umbellata Schkuhr. Hanover, Havana, and Dixon areas, most abundant in the *Panicum pseudopubescens* association, persisting as a relic on the windward slopes, occasional in the bunch-grass association, and rare on the deposits of blowouts.

Carex pennsylvanica Lam. Oquawka area, in the bunch-grass association; Winnebago area, in open places in the black oak association.

Carex sp. Dixon area, in the Solidago association.

Commelinaceae

Commelina virginica L. Havana and Oquawka areas; one of the most abundant interstitial species, growing in a wide variety of associations, but probably most abundant on blowout deposits.

Tradescantia reflexa Raf. Hanover, Kankakee, Winnebago, Amboy, Havana, and Oquawka areas; common in the bunch-grass and black oak associations and persisting as a relic in the bur oak and *Panicum pseudopubescens* associations.

Juncaceae

Juncus tenuis Willd. Havana area, in the *Solidago* association; Winnebago area, in open places in the black oak association.

Juncus nodosus L. Dixon area, in the swamp association.

Juncus acuminatus Michx. Dixon and Havana areas, in the *Solidago* association, and also less frequently in the *Polytrichum* and *Salix* associations.

Liliaceae

Lilium philadelphicum L., var., *andinum* (Nutt.) Ker. Winnebago area, in the bur oak association.

Asparagus officinalis L. Havana area, in the mixed forest association.

Smilacina racemosa (L.) Desf. Hanover area, in the dune thicket association; Winnebago area, in the bur oak association; Havana area, in the mixed forest association, and occasionally in the black oak association.

Smilacina stellata (L.) Desf. Hanover, Winnebago, Amboy, and Havana areas, characteristic of the black oak association, and in the last area rarely also in the mixed forest association.

Polygonatum commutatum (R. & S.) Dietr. Hanover, Winnebago, Amboy, Oquawka, and Havana areas, characteristic of the bur oak and mixed forest associations, one of the earliest pioneers in the black oak forest, indicating the succession, and occasional in the blowout and dune thickets.

Smilax herbacea L. Hanover, Winnebago, Amboy, and Havana areas, chiefly in the bur oak and mixed forest associations, occasional as a pioneer in the black oak association, and in the Hanover area in the dune thickets.

Smilax cirrhata (Engelm.) Wats. Hanover, Winnebago, and Amboy areas, in the bur oak association, or as a pioneer in the black oak forest.

Smilax hispida Muhl. In the dune thickets in the Hanover area, mixed forest in the Oquawka area, and in the black oak and bur oak forest in the Amboy area.

Dioscoreaceae

Dioscorea villosa L. Havana area, in the mixed forest association.

Amaryllidaceae

Hypoxis hirsuta (L.) Coville. Hanover area, under oaks on the perched dunes.

Iridaceae

Sisyrinchium sp. Hanover and Oquawka areas, in the bunchgrass association and persisting as a relic in the *Panicum pseudopubescens* association.

Orchidaceae

Cypripedium parviflorum Salisb., var. *pubescens* (Willd.) Knight. Winnebago area, in the bur oak association.

Spiranthes cernua (L.) Richard. Dixon area, in the *Polytrichum* association.

Salicaceae

Salix nigra Marsh. Dixon area, in the *Salix* association.

Salix longifolia Muhl. Dixon and Havana areas, in the *Salix* association; Hanover area, in the dune thickets.

Salix pedicellaris Pursh. Dixon area, in the *Polytrichum* association.

Salix tristis Ait. Winnebago and Amboy areas, in the black oak association and as a relic in the bur oak forests; Havana area, in the mixed forest association.

Populus alba L. Oquawka area, frequently planted and escaped along roadsides and fence-rows.

Populus tremuloides Michx. Winnebago, Amboy, and Kankakee areas, in the swamps and meadows between the sand hills, and occasional in the bur oak association.

Populus grandidentata Michx. Amboy area, in the bur oak association, or occasionally as a pioneer in the black oak woods.

Populus deltoides Marsh. Hanover area, in the dune thickets; Dixon area, in the *Salix* association; Oquawka and Havana areas, in blowout thickets.

Juglandaceae

Juglans nigra L. Hanover area, in the dune thickets; Oquawka area, in the mixed forest association on the river dune.

Carya ovata (Mill.) K. Koch. Winnebago area, in the bur oak association.

Carya cordiformis (Wang.) K. Koch. Hanover area, in the mixed forest; Oquawka and Havana areas, in the black oak association and persisting in the mixed forest.

Betulaceae

Corylus americana Walt. Hanover area, on the perched dunes; Winnebago and Amboy areas, common in the bur oak association and occasional as a pioneer in the black oak forest.

Betula nigra L. Hanover and Oquawka areas, in the mixed forest association near the river.

Betula alba L., var. *papyrifera* (Marsh.) Spach. Hanover area, on the perched dunes.

Fagaceae

Quercus alba L. Winnebago area, in the bur oak association.

Quercus macrocarpa Michx. Winnebago and Amboy areas, the characteristic species of the bur oak association.

Quercus rubra L. Oquawka area, in the mixed forest association.

Quercus velutina Lam. Hanover, Winnebago, Amboy, Kankakee, Havana, and Oquawka areas, the characteristic species of the black oak association, persisting commonly as a relic in the mixed forest association and less commonly in the bur oak forest; common on the perched dunes in the Hanover area.

Quercus marilandica Muench. Havana and Oquawka areas, abundant in the black oak association, and persisting in the mixed forest.

Urticaceae

Ulmus americana L. Hanover and Oquawka areas, in the mixed forest association and in the dune thickets.

Celtis occidentalis L. Hanover and Havana areas, in the mixed forest association, and in the blowout and dune thickets.

Morus rubra L. Havana area, in the mixed forest association.

Boehmeria cylindrica (L.) Sw. Havana area, in the *Salix* association.

Parietaria pennsylvanica Muhl. Oquawka area, in the mixed forest association.

Santalaceae

Comandra umbellata (L.) Nutt. Hanover, Winnebago, Amboy, Oquawka, and Hanover areas, in the black oak association, or occasionally along roadsides.

Polygonaceae

Rumex altissimus Wood. Hanover area, in the black oak association.

Rumex Acetosella L. Hanover, Winnebago, Dixon, and Oquawka areas, a common interstitial in the bunch-grass association, and in cultivated ground, less frequently in the *Panicum pseudopubescens* association.

Rumex sp. Hanover area, in the blowsand association.

Polygonum aviculare L. Oquawka area, a weed along roadsides and in yards.

Polygonum erectum L. Oquawka area, a common roadside weed.

Polygonum tenue Michx. Hanover, Oquawka, and Havana areas, a common interstitial in the bunch-grass association and less commonly also in the *Panicum pseudopubescens* association.

Polygonella articulata (L.) Meisn. Hanover and Dixon areas, in the blowsand association; Hanover and Oquawka areas, in open places in the black oak association.

Chenopodiaceae

Cycloloma atriplicifolium (Spreng.) Coult. Havana and Oquawka areas, in the blowsand and deposit associations.

Chenopodium album L. Hanover, Havana, and Oquawka areas, common as a weed, occasional in the bunch-grass association and in open places in the black oak forest.

Amaranthaceae

Froelichia floridana (Nutt.) Moq. Dixon, Oquawka, and Havana areas, usually in the blowsand association, occasionally an interstitial in the bunch-grass association or open blowout deposits; Hanover area, along the railroad track, appearing as if introduced.

Phytolaccaceae

Phytolacca decandra L. Oquawka area, in waste places under the shade of trees.

Nyctaginaceae

Oxybaphus nyctagineus (Michx.) Sweet. Hanover, Dixon, and Oquawka areas, in the blowsand and blowout thicket associations, an interstitial in the bunch-grass, and frequent as a weed in waste places and along roads.

Illecebraceae

Anychia polygonoides Raf. Hanover, Havana, and Oquawka areas, in the black oak association.

Anychia canadensis (L.) BSP. Oquawka area, in the mixed forest association.

Aizoaceae

Mollugo verticillata L. Hanover, Dixon, Oquawka, and Havana areas, especially common in the blowsand association and occasional as an interstitial in the bunch-grass and *Panicum pseudopubescens* associations.

Caryophyllaceae

Arenaria lateriflora L. Winnebago area, in the bur oak association.

Silene antirrhina L. Hanover, Winnebago, Dixon, Havana, and Oquawka areas, an abundant weed in fields and a common interstitial in the bunch-grass and *Panicum pseudopubescens* associations.

Silene stellata (L.) Ait. f. Hanover, Winnebago, Havana, and Oquawka areas, characteristic of the bur oak and mixed forest associations and a pioneer in the black oak association.

Saponaria officinalis L. Hanover area, in the black oak association near dwellings.

Portulacaceae

Talinum rugospermum Holzinger. Winnebago, Oquawka, and Havana areas, in the black oak association; Hanover area, in the bunch-grass association.

Ranunculaceae

Ranunculus abortivus L. Hanover area, in the mixed forest association.

Anemone patens L., var. *Wolfgangiana* (Bess.) Koch. Hanover area, on the perched dunes.

Anemone caroliniana Walt. Hanover area, in the bunch-grass association.

Anemone cylindrica Gray. Hanover and Oquawka areas, in the bunch-grass and black oak associations; Winnebago and Amboy areas, in the black oak association.

Anemone virginiana L. Havana area, in the mixed forest association and appearing as a pioneer in the black oak association.

Anemone canadensis L. Oquawka area, in the mixed forest association.

Aquilegia canadensis L. Hanover and Oquawka areas, in the mixed forest association.

Delphinium Penardi Huth. Oquawka area, in the bunch-grass association.

Menispermaceae

Menispermum canadense L. Hanover area, in the dune thicket and mixed forest associations; Havana area, in the blowout thicket association.

Fumariaceae

Corydalis micrantha (Engelm.) Gray. Hanover area, in the blowout association on the river dune.

Cruciferae

Draba caroliniana Walt. Hanover area, in the bunch-grass association, and in sheltered places in the blowsand association on the river dune.

Lesquerella argentea (Pursh) MacM. Havana area, in the bunch-grass association.

Lepidium virginicum L. Hanover, Winnebago, Dixon, Oquawka, and Havana areas, especially abundant in the *Panicum pseudopubescens* association, a common interstitial in the bunch-grass association, occasional in the blowsand association, and common in open places in the black oak association.

Erysimum parviflorum Nutt. Havana area, in the bunch-grass association.

Arabis lyrata L. Hanover, Winnebago, and Oquawka areas, most abundant as an interstitial in the bunch-grass and *Panicum pseudopubescens* associations in the Hanover area, also in open places in the black oak association.

Capparidaceae

Polanisia graveolens Raf. Hanover, Oquawka, and Havana areas, frequent in the blowsand association and in the black oak forest.

Cristatella Jamesii T. & G. Hanover and Havana areas, in the blowsand association.

Saxifragaceae

Heuchera hispida Pursh. Winnebago area, in the bur oak association; Hanover and Oquawka areas, in the mixed forest association.

Ribes gracile Michx. Hanover and Havana areas, in the mixed forest association, occasional in the dune thickets and the black oak forest, or along fence-rows on the prairie.

Rosaceae

Spiraea salicifolia L. Dixon area, in the *Solidago* association.

Pyrus ioensis (Wood) Bailey. Hanover area, in the dune thickets.

Pyrus Malus L. Hanover area, in the blowout thicket association.

Pyrus americana (Marsh.) DC. Winnebago area, in the black oak association.

Fragaria virginiana Duchesne, var. *illinoensis* (Prince) Gray. Winnebago and Amboy areas, in the black oak association and as a relic in the bur oak association; Hanover area, in the mixed forest.

Fragaria vesca L., var. *americana* Porter. Winnebago area, in the bur oak association; Hanover area, on the perched dunes.

Potentilla arguta Pursh. Winnebago and Amboy areas, in the black oak association and along roadsides.

Potentilla argentea L. Winnebago area, in a pastured field.

Potentilla canadensis L. Winnebago area, in the black oak association.

Geum canadense Jacq. Hanover area, in the mixed forest association.

Rubus idaeus L., var. *aculeatissimus* (C. A. Mey.) Regel & Tiling. Hanover area, in the mixed forest association; Winnebago area, in the bur oak association.

Rubus occidentalis L. Hanover area, in the black oak and mixed forest associations and on the perched dunes; Winnebago area, in the black oak and bur oak associations.

Rubus sp. (Blackberry). Amboy area, in the bur oak association.

Agrimonia mollis (T. & G.) Britton. Winnebago and Amboy areas, in the bur oak association; Havana area, in the mixed forest association.

Rosa humilis Marsh. Hanover area, in the black oak and blowout thicket associations; Winnebago area, in the black oak forest and as a relic in the bur oak association; Dixon area, in the bunchgrass association.

Prunus serotina Ehrh. Hanover area, in the dune thickets; Winnebago area, in the bur oak association and as a pioneer in the black oak forest; Havana area, in the mixed forest association.

Prunus virginiana L. Hanover area, in the mixed forest and

dune thicket associations; Winnebago area, in the bur oak association; in both areas as a pioneer in the black oak association.

Prunus sp. (Plum). Hanover area, in the dune thickets.

Leguminosae

Gymnocladus dioica (L.) Koch. Havana area, in the mixed forest association.

Gleditsia triacanthos L. Hanover area, in the dune thicket association; Dixon area, planted on the deposits of a blowout; Oquawka area, along roadsides.

Cassia Chamaechrista L. Most abundant in the Havana and Oquawka areas, in the bunch-grass, blowsand, and black oak associations; Hanover area, in the blowsand association; Amboy area, in the black oak forest; Dixon area, in the *Solidago* association.

Cercis canadensis L. Oquawka area, in the mixed forest association.

Baptisia bracteata (Muhl.) Ell. Winnebago area, in the black oak association; Oquawka area, in the bunch-grass and *Panicum pseudopubescens* associations.

Lupinus perennis L. Winnebago and Amboy areas, in the black oak association; Kankakee area, in mucky meadows at the base of sand hills.

Trifolium pratense L. Oquawka area, roadsides.

Trifolium repens L. Oquawka area, along roadsides.

Amorpha canescens Pursh. Hanover, Winnebago, Amboy, Dixon, Kankakee, Oquawka, and Havana areas, most abundant in and typical of the bunch-grass association, persistent as a relic and common in the black oak association, and occasional in the bur oak and mixed forest associations; in the Hanover area, also on the perched dunes.

Petalostemum purpureum (Vent.) Rydb. Hanover and Oquawka areas, abundant in the bunch-grass; also in the black oak association in the Amboy and Oquawka areas; along roadsides in the Winnebago area.

Petalostemum candidum Michx. Hanover and Oquawka areas, in the bunch-grass association; Winnebago and Amboy areas, in the black oak association.

Tephrosia virginiana (L.) Pers. In all seven areas; abundant in the bunch-grass and black oak associations, frequent on blowout deposits, and occasional in the blowsand and *Panicum pseudopubescens* associations.

Robinia Pseudo-Acacia L. Oquawka area, commonly planted as

a sand-binder and escaping into the mixed forest and blowout thicket associations.

Desmodium grandiflorum (Walt.) DC. Winnebago area, in the bur oak association.

Desmodium illinoense Gray. Oquawka area, in the bunch-grass association; Amboy area, in the black oak forest.

Lespedeza capitata Michx. Common in all seven areas, chiefly in the bunch-grass and black oak associations; a relic in the *Panicum pseudopubescens* association, active in the stabilization of all parts of the blowouts; in the Dixon area it appears in the *Solidago* association; and in the Hanover area, on the perched dunes.

Strophostyles helvola (L.) Britton. Havana area, in the black oak forest; Oquawka area, in the bunch-grass, blowsand, black oak, and mixed forest associations.

Strophostyles sp. Havana area, in the bunch-grass association.

Amphicarpa Pitcheri T. & G. Hanover area, in the mixed forest association; Winnebago area, in the bur oak association.

Linaceae

Linum sulcatum Riddell. Hanover and Oquawka areas, in the bunch-grass association.

Oxalidaceae

Oxalis corniculata L. Hanover area, in the bunch-grass and black oak associations.

Geraniaceae

Geranium maculatum L. Winnebago area, in the bur oak association.

Rutaceae

Zanthoxylum americanum Mill. Oquawka area, in the mixed forest association.

Polygalaceae

Polygala polygama Walt. Hanover, Winnebago, Dixon, and Oquawka areas, in the bunch-grass, *Panicum pseudopubescens*, and black oak associations.

Polygala incarnata L. Oquawka area, in the bunch-grass association.

Polygala sanguinea L. Dixon area, in the *Solidago* association,

and as a relic also in the *Polytrichum* association; Amboy area, in muck meadows at the base of the dunes.

Polygala verticillata L. Hanover, Havana, and Oquawka areas, in the bunch-grass and *Panicum pseudopubescéns* associations.

Euphorbiaceae

Croton glandulosus L., var. *septentrionalis* Muell. Arg. Hanover, Havana, and Oquawka areas, an interstitial in the bunch-grass and *Panicum pseudopubescens* associations, common in the blowsand association, and occasional on blowout deposits.

Crotonopsis linearis Michx. Havana area, a common interstitial in the bunch-grass, *Panicum pseudopubescens,* blowsand, deposit, and black oak associations.

Euphorbia Geyeri Engelm. Hanover, Dixon, Havana, and Oquawka areas, most abundant in the blowsand association, occasional as an interstitial in the bunch-grass and the black oak forest.

Euphorbia corollata L. Very abundant in all seven areas, chiefly in the bunch-grass and black oak association, frequent on blowout deposits, occasional in the blowsand association, and rare in the bur oak association.

Anacardiaceae

Rhus glabra L. Winnebago and Amboy areas, in the bur oak association; Hanover area, in the mixed forest association.

Rhus Toxicodendron L. Hanover, Oquawka, and Havana areas, in the mixed forest association, in the dune thickets, and occasionally a pioneer in the black oak forest; Winnebago area, in the bur oak and black oak associations.

Rhus canadensis Marsh., var. *illinoensis* (Greene) Fernald. Hanover, Havana, and Oquawka areas, in the bunch-grass, deposit, and black oak associations.

Celastraceae

Celastrus scandens L. Havana and Oquawka areas, in the mixed forest; Hanover area, in the dune thickets.

Aceraceae

Acer saccharinum L. Oquawka area, in the mixed forest association on the river dune.

Acer Negundo L. Havana area, in the blowout thicket association.

Rhamnaceae

Ceanothus americanus L. Hanover, Winnebago, Amboy, Oquawka, and Hanover areas, in the black oak, bur oak, and mixed forest associations; occasional in the bunch-grass in the Oquawka area.

Ceanothus ovatus Desf. Hanover area, in the bunch-grass, deposit, and black oak associations.

Vitaceae

Psedera quinquefolia (L.) Greene. Winnebago area, in the bur oak association; Hanover, Havana, and Oquawka areas, in the mixed forest, blowout thicket, and dune thicket associations, and one of the most frequent pioneers in the black oak association.

Vitis vulpina L. Winnebago and Amboy areas, in the bur oak association; Havana, Oquawka, and Hanover areas, in the mixed forest, the blowout thickets, and the dune thickets, and occasional as a pioneer in the black oak association.

Malvaceae

Callirhoe triangulata (Leavenw.) Gray. Hanover and Havana areas, chiefly in the bunch-grass and the black oak forests, and occasionally in the *Panicum pseudopubescens* association.

Hypericaceae

Hypericum cistifolium Lam. Oquawka area, in the mixed forest association along the river dune.

Hypericum mutilum L. Havana area, in the *Solidago* association.

Hypericum majus (Gray) Britton. In the *Polytrichum* association in the Dixon area.

Hypericum gentianoides (L.) BSP. Dixon area, in the *Polytrichum* association, or perhaps more common in a zone just outside of it.

Cistaceae

Helianthemum majus BSP. Hanover, Winnebago, Amboy, Dixon, Havana, and Oquawka areas, probably most widely distributed in the black oak association, but also abundant in the bunch-grass.

Hudsonia tomentosa Nutt. Hanover and Dixon areas, charac-

teristic of the *Hudsonia* association, and occasional upon blowout deposits and in black oak woods.

Lechea sp. In the black oak association in the Winnebago and Oquawka areas.

Violaceae

Viola pedata L. Hanover, Oquawka, and Winnebago areas, most abundant in the bunch-grass prairie and in the black oak woods, occasional in the *Panicum pseudopubescens* association and on blowout deposits.

Viola lanceolata L. Dixon area, in the *Polytrichum* association; Kankakee area, in the wet meadows.

Cactaceae

Opuntia Rafinesquii Engelm. Hanover, Oquawka, and Havana areas, usually very abundant in the bunch-grass and the open parts of the black oak forest.

Opuntia fragilis (Nutt.) Haw. Hanover area, in the bunch-grass and *Panicum pseudopubescens* associations.

Melastomaceae

Rhexia virginica L. Dixon area, in the *Polytrichum* and *Solidago* associations; Amboy area, in the wet meadows.

Onagraceae

Ludvigia alternifolia L. Havana area, in the *Salix* association.

Ludvigia palustris (L.) Ell. Dixon and Havana areas, in the swamp association, and persistent as a relic in the *Solidago* and *Polytrichum* associations.

Oenothera biennis L. In the bur oak association in the Winnebago area, and in the mixed forest in the Havana area.

Oenothera rhombipetala Nutt. One of the most common interstitials, occurring in all seven areas in a wide variety of associations, but most abundant in the bunch-grass and in the *Panicum pseudopubescens* association.

Circaea lutetiana L. In the bur oak forest in the Winnebago area.

Umbelliferae

Sanicula canadensis L. Winnebago and Havana areas, in the bur oak and mixed forest associations.

Zizia aurea (L.) Koch. Winnebago area, in the black oak forest; Hanover area, in the mixed forest.

Cornaceae

Cornus Baileyi Coult. & Evans. Hanover, Winnebago, Amboy, Havana, and Oquawka areas, in the bur oak and mixed forest associations; also in the dune thickets and the blowout thickets.

Ericaceae

Pyrola elliptica Nutt. In the bur oak association in the Winnebago area.

Monotropa uniflora L. Winnebago area, in the black oak forest, probably a pioneer from the bur oak association.

Primulaceae

Steironema lanceolatum (Walt.) Gray. Winnebago area, in the swamp association.

Dodecatheon Meadia L. Winnebago area, in the bur oak association.

Oleaceae

Fraxinus pennsylvanica Marsh., var. *lanceolata* (Borkh.) Sarg. Hanover and Oquawka areas, in the mixed forest and dune thicket associations and as a pioneer in the black oak forest.

Apocynaceae

Apocynum androsaemifolium L. Winnebago and Amboy areas, in the black oak forest and persisting as a relic in the bur oak association; Hanover area, in the mixed forest.

Apocynum cannabinum L., var. *hypericifolium* (Ait.) Gray. In blowsand in the Dixon area.

Asclepiadaceae

Asclepias tuberosa L. Hanover, Havana, and Amboy areas, in the black oak forest; Oquawka area, in the mixed forest; Winnebago area, along a sandy roadside.

Asclepias syriaca L. Hanover and Oquawka areas, near cultivated grounds around the river dune; Havana area, in the black oak and *Solidago* associations.

Asclepias amplexicaulis Sm. In the black oak forest in the Hanover, Winnebago, Amboy, Havana, and Oquawka areas; also in the bunch-grass association in the Dixon and Oquawka areas.

Asclepias phytolaccoides Pursh. Hanover and Havana areas, in the mixed forest association.

Asclepias verticillata L. In the black oak and bur oak forests in the Havana area, and along roadsides in the Hanover area.

Acerates floridana (Lam.) Hitchc. In the windward slope association in the Dixon area, probably a relic from the bunch-grass association.

Acerates viridiflora Ell. Hanover and Oquawka areas, in the bunch-grass and basin associations, and occasional in the *Panicum pseudopubescens* association; Winnebago area, in an open place in the black oak forest.

Acerates viridiflora Ell., var. *lanceolata* (Ives) Gray. Hanover and Havana areas, characteristic of the basin association, and occasional in the bunch-grass and *Panicum pseudopubescens* associations.

Acerates viridiflora Ell., var. *linearis* Gray. Hanover and Oquawka areas, in the basin and blowsand associations.

Convolvulaceae

Breweria Pickeringii (M. A. Curtis) Gray. In the bunch-grass prairies of the Oquawka area.

Ipomoea hederacea Jacq. A weed in cultivated fields in the Oquawka area.

Polemoniaceae

Phlox pilosa L. Perched dunes in the Hanover area.

Phlox bifida Beck. In the bunch-grass and black oak associations in the Havana and Winnebago areas.

Boraginaceae

Lappula virginiana (L.) Greene. Havana area, in the mixed forest association.

Lithospermum Gmelini (Michx.) Hitchc. Abundant in all seven areas, chiefly in the bunch-grass and black oak associations, more rarely in the basin, blowsand, and *Panicum pseudopubescens* associations.

Lithospermum angustifolium Michx. In the bunch-grass association in the Havana area.

Verbenaceae

Verbena stricta Vent. Havana, Oquawka, Dixon, and Hanover areas, occasional in the bunch-grass and black oak forest, and a weed along roadsides.

Verbena bracteosa Michx. Perched dunes and bunch-grass in the Hanover area.

Labiatae

Teucrium canadense L. Havana and Hanover areas, in the black oak and *Solidago* associations.

Teucrium occidentale Gray. Hanover area, an interstitial in the bunch-grass, and common in the blowsand association along the river dune.

Scutellaria parvula Michx. In the black oak association in the Hanover, Amboy, and Havana areas; also an interstitial in the bunch-grass in the Hanover area, and in the blowsand association in the Dixon area.

Nepeta Cataria L. Hanover area, in the black oak forest near dwellings.

Physostegia denticulata (Ait.) Britton. Oquawka, Havana, and Hanover areas, in the bunch-grass and black oak associations.

Leonurus Cardiaca L. Hanover area, near dwellings in the black oak forest.

Monarda fistulosa L. Oquawka area, in the black oak and mixed forest associations.

Monarda mollis L. Hanover, Winnebago, Amboy, Havana, and Oquawka areas, usually in the bur oak forest, but occasionally as a pioneer in the black oak association.

Monarda punctata L. Hanover, Dixon, Havana, Oquawka, and Kankakee areas, one of the most abundant interstitials in the bunch-grass, and common also in the *Panicum pseudopubescens* and blowsand associations and in open places in the black oak forest; very common as a weed in pastured ground.

Hedeoma hispida Pursh. Hanover, Dixon, and Oquawka areas, an interstitial in the bunch-grass, and common also in the *Panicum pseudopubescens* and blowsand associations.

Lycopus americanus Muhl. Havana area, in the *Salix* association; Dixon area, in the *Polytrichum* association; Amboy area, in the wet meadows.

Solanaceae

Solanum nigrum L. Hanover, Oquawka, and Havana areas, under the shade of trees.

Solanum carolinense L. Hanover and Oquawka areas, in the black oak forest and a weed in cultivated fields.

Physalis heterophylla Nees. Hanover, Winnebago, Dixon, and Havana areas, in the bunch-grass and black oak associations.

Physalis virginiana Mill. Hanover and Oquawka areas, in the black oak and bunch-grass associations.

Scrophulariaceae

Verbascum Thapsus L. Hanover, Winnebago, Oquawka, and Havana areas, usually in the black oak forest, but occasionally in the bunch-grass association.

Linaria canadensis (L.) Dumont. Hanover, Dixon, Oquawka, and Havana areas, a common interstitial in the bunch-grass, frequent in the *Panicum pseudopubescens* and blowsand associations, and occasional on blowout deposits.

Scrophularia leporella Bicknell. Hanover, Winnebago, Oquawka, and Havana areas, most abundant in the mixed forest and in the dune thickets, less frequent in the black oak forest.

Pentstemon hirsutus (L.) Willd. Hanover, Amboy, Havana, and Oquawka areas, common in the bunch-grass and the black oak forest, and occasional in the *Panicum pseudopubescens* and bur oak associations.

Pentstemon grandiflorus Nutt. In the bunch-grass and black oak associations of the Oquawka area.

Veronica virginica L. Winnebago and Amboy areas, in the bur oak association.

Synthyris Bullii (Eaton) Heller. Hanover, Winnebago, and Oquawka areas, characteristic of the black oak association and occasional as a relic in the bur oak forest, rare in the bunch-grass.

Gerardia grandiflora Benth. In the black oak association in the Winnebago and Amboy areas, and as a relic in the bur oak forest.

Gerardia purpurea L. In the *Solidago* association in the Dixon area.

Castilleja coccinea (L.) Spreng. Winnebago area, in the black oak association.

Pedicularis canadensis L. Winnebago area, in the black oak and bur oak associations.

Orobanchaceae

Orobanche fasciculata Nutt. Parasitic on *Artemisia caudata* in the bunch-grass association of the Hanover area.

Acanthaceae

Ruellia ciliosa Pursh. Havana and Oquawka areas, in the bunch-grass and black oak associations.

Plantaginaceae

Plantago Rugelii Dene. Along roadsides in the Oquawka area.

Rubiaceae

Galium pilosum Ait. In the black oak forest in the Havana area.

Galium concinnum T. & G. Winnebago area, in the bur oak association; Havana area, in the mixed forest.

Diodia teres Walt. Hanover and Havana areas, common in the blowsand association, and occasional in the black oak forest and as a weed in cultivated ground.

Caprifoliaceae

Lonicera Sullivantii Gray. Winnebago area, in the bur oak association.

Campanulaceae

Specularia perfoliata (L.) A. DC. Hanover, Havana, and Winnebago areas, a common interstitial in the bunch-grass, occasional in open places in the black oak forest and one of the most abundant weeds in sandy fields.

Compositae

Vernonia fasciculata Michx. Havana area, in the *Solidago* association; Amboy area, in the wet meadows between the dunes; Hanover area, in pastured bunch-grass.

Eupatorium purpureum L. Havana area, in the mixed forest association; Amboy area, in the wet meadows at the base of the dunes.

Eupatorium serotinum Michx. Hanover area, in the black oak and mixed forest associations.

Eupatorium urticaefolium Reichard. In the mixed forest association in the Hanover and Havana areas.

Kuhnia eupatorioides L., var. *corymbulosa* T. & G. Hanover, Oquawka, and Havana areas, chiefly in the bunch-grass, but occasional in the blowsand and dune thicket associations.

Liatris cylindracea Michx. Hanover area, in the bunch-grass association; Winnebago and Amboy areas, in the black oak forest.

Liatris scariosa Willd. In the bunch-grass association in the Hanover, Dixon, Oquawka, and Havana areas; in the black oak forest in the Winnebago and Amboy areas.

Chrysopsis villosa Nutt. Hanover, Dixon, and Havana areas, common in the bunch-grass association; along roadsides in the Amboy area.

Solidago speciosa Nutt., var. *angustata* T. & G. Winnebago, Amboy, Hanover, and Havana areas, in the black oak forest; Hanover and Oquawka areas, in the bunch-grass association.

Solidago missouriensis Nutt. In the bunch-grass association in the Havana and Hanover areas.

Solidago nemoralis Ait. Abundant in all seven areas, in the black oak and bunch-grass associations; in the Hanover area, also in the *Panicum pseudopubescens* association.

Solidago serotina Ait. Hanover and Havana areas, in the black oak association.

Solidago rigida L. In the bunch-grass association in the Hanover area; along roadsides in the Amboy area.

Solidago graminifolia (L.) Salisb. Characteristic of the *Solidago* association in the Dixon and Havana areas; along sandy roadsides in the Amboy area; in a swamp between the dunes in the Winnebago area.

Aster oblongifolius Nutt. Oquawka area, in the mixed forest on the river dune.

Aster sericeus Vent. In the bunch-grass association in the Hanover, Havana, and Oquawka areas; in the black oak forest in the Hanover and Amboy areas; in the mixed forest on the river dune in the Oquawka area; in a cleared field in the Winnebago area.

Aster azureus Lindl. Winnebago, Amboy, Havana, and Oquawka areas, in the black oak association.

Aster multiflorus Ait. Havana, Oquawka, and Hanover areas, in the bunch-grass association.

Aster linariifolius L. Common in all seven areas in the bunch-grass and black oak associations, and occasionally persisting as a relic in the *Panicum pseudopubescens* association.

Aster sp. In the bunch-grass association in the Hanover area.

Aster sp. Dixon area, in the *Polytrichum* association.

Erigeron pulchellus Michx. On the perched dunes in the Hanover area.

Erigeron ramosus (Walt.) BSP. Hanover and Oquawka areas, in the bunch-grass and *Panicum pseudopubescens* associations; Winnebago area, in the black oak forest.

Erigeron canadensis L. An interstitial in the bunch-grass in the Hanover area, and on blowout deposits in the Oquawka area.

Antennaria plantaginifolia (L.) Richards. Hanover area, in the mixed forest association.

Antennaria sp. One or more unidentified species of *Antennaria* are common in the bunch-grass and black oak forests of the Hanover, Winnebago, Amboy, Dixon, Oquawka, and Havana areas.

Gnaphalium polycephalum Michx. Hanover area, in the bunch-grass; Amboy and Oquawka areas, in the black oak forest; in the latter area also in the *Stenophyllus* and blowout thicket associations.

Silphium laciniatum L. Along roadsides in the Amboy area.

Silphium integrifolium Michx. Amboy area, in the black oak forest.

Parthenium integrifolium L. Hanover area, in the mixed forest association; Amboy area, along sandy roadsides.

Ambrosia artemisiifolia L. A weed in the waste grounds in the Oquawka and Winnebago areas.

Ambrosia psilostachya DC. Observed in the Hanover, Winnebago, Dixon, Oquawka, and Havana areas, and probably in the others as well; a common interstitial in the bunch-grass, black oak, and *Panicum pseudopubescens* associations, and abundant in the blowsand association.

Xanthium commune Britton. A weed in sandy fields in the Oquawka area.

Rudbeckia hirta L. Hanover, Winnebago, Havana, and Oquawka areas, abundant in the black oak forest, and occasional in the mixed forest and bunch-grass.

Brauneria pallida (Nutt.) Britton. Hanover, Dixon, and Oquawka areas, in the bunch-grass association; Amboy area, along roadsides.

Lepachys pinnata (Vent.) T. & G. Winnebago area, in a clearing in the black oak forest.

Helianthus lenticularis Dougl. Oquawka area, in the blowsand association.

Helianthus scaberrimus Ell. Hanover and Oquawka areas, common in the bunch-grass and *Panicum pseudopubescens* associations; Amboy area, along sand roadsides.

Helianthus occidentalis Riddell. Common in all seven areas in the bunch-grass and black oak associations.

Helianthus occidentalis Riddell, var. *illinoensis* (Gleason) Gates. With the species, especially in more shaded places; occasional in the mixed forest association.

Helianthus strumosus L. Winnebago, Amboy, and Havana areas, in the black oak forest, and persisting as a relic in the bur oak and mixed forest associations.

Coreopsis palmata Nutt. Hanover, Winnebago, Amboy, and Oquawka areas, in the bunch-grass and black oak associations, rare as a relic in the bur oak forest; Havana area, in the mixed forest.

Hymenopappus carolinensis (Lam.) Porter. In the black oak association in the Kankakee area.

Achillea Millefolium L. Winnebago, Amboy, Dixon, and Oquawka areas, in the bunch-grass and black oak associations.

Anthemis Cotula L. A weed in the Oquawka area.

Artemisia caudata Michx. Very common in all seven areas in the bunch-grass and black oak associations, occasional as a relic in the *Panicum pseudopubescens* association.

Artemisia ludoviciana Nutt. Hanover area, occasional in the bunch-grass and black oak forest; more abundant in shaded places along fence-rows and thickets.

Cacalia atriplicifolia L. Hanover area, on the perched dunes; Winnebago area, in the bur oak forest; Havana area, in the black oak and mixed forest associations, and occasionally in the bunch-grass.

Senecio Balsamitae Muhl. Hanover and Oquawka areas, in the bunch-grass and black oak associations.

Krigia virginica (L.) Willd. Havana area, in the black oak association.

Krigia amplexicaulis Nutt. In the bur oak forest in the Winnebago area.

Lactuca scariola L., var. *integrata* Gren. & Godr. Oquawka area, in the *Stenophyllus* association.

Lactuca canadensis L. Hanover, Havana, and Oquawka areas, in the bunch-grass, occasional in the blowout thickets and the black oak forest.

Prenanthes alba L. Winnebago area, in the bur oak association, or as a pioneer in the black oak forest.

Hieracium longipilum Torr. In the black oak forest in the Winnebago area.

Hieracium canadense Michx. Hanover area, in the black oak association.

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ERRATA

PLATE III, Fig. 1, after the word *mixed* in legend insert *consocies of the*.

PLATE IX, Fig. 2, dele the legend and read instead: Root-system of *Tephrosia virginiana*, exposed by blowing of the sand.

PLATE X, Fig. 2, dele the legend and read instead: A blowout almost stabilized by bunch-grasses, especially *Leptoloma cognatum*.

PLATE I.

Fig. 1. General view of the sand-dunes near Havana. The isolated trees are *Quercus velutina*; at the right is a grove of *Juglans nigra*.

Fig. 2. *Leptoloma cognatum* consocies of the bunch-grass association, Oquawka area. Large bunches of *Andropogon scoparius* in the rear, and a flowering *Achillea Millefolium* in the center.

PLATE II.

Fig. 1. Mixed consocies of the bunch-grass association in the Hanover area, *Andropogon scoparius* most abundant.

Fig. 2. Mixed consocies of the bunch-grass association in the Hanover area. Various species of grasses and perennials in the foreground, and a society of *Ceanothus ovatus* behind.

PLATE III.

Fig. 1. Luxuriant development of the mixed bunch-grass association in a depression between dunes in the Hanover area.

Fig. 2. Typical development of the *Panicum pseudopubescens* association, Hanover area.

PLATE IV.

Fig. 1. Typical blowout in the Hanover area, looking west. In the foreground, the deposit association, with *Panicum virgatum* dominant and many interstitials; behind this, the blowsand association, with *Diodia teres*; next, the basin, with a few plants of *Acerates*. The dunes at the side are held by *Rhus*.

Fig. 2. Blowout complex in the Hanover area, looking north. Bunches of *Panicum virgatum* are conspicuous. Typical habitat for *Cristatella Jamesii*.

PLATE V.

The deposits of the blowout shown in Plate VIII, Fig. 1. The bunch-grass association at the right.

PLATE VI.

Fig. 1. Young blowout in the Hanover area, looking north, indicating the differentiation of three associations. Detached bunches of *Panicum pseudopubescens* at the left, mark the windward slope; the deposits at the right are occupied with *Panicum virgatum*; while the basin has as yet no vegetation.

Fig. 2. *Acerates viridiflora*, var. *lanceolata*, in its typical habitat.

PLATE VII.

Fig. 1. Incipient blowout on a hillside in the bunch-grass association, Hanover area. The windward slope is just developing in the background, while an extensive growth of *Panicum virgatum*, indicating the deposits, occupies the center. *Rhus* is in the foreground, at the right.

Fig. 2. Large blowout in the Hanover area, looking east. The dunes at the right are held by *Rhus*, *Tephrosia*, and *Panicum virgatum*, by *Tephrosia* alone at the left, and by *Tephrosia* and *Panicum* at the rear. The basin is almost bare.

Fig. 1. Large blowout in the river dune, Hanover area, looking east. The dunes at the left are held by *Rhus*; those at the right by *Prunus*, with various herbs in the blowsand association at their base. The basin is entirely bare.

Fig. 2. Seedlings of *Diodia teres* coming up in wagon tracks. Thickets of *Rhus* and bunches of *Panicum virgatum* at the rear.

PLATE IX.

Fig. 1. Characteristic growth of *Tephrosia virginiana*.

Fig. 2. A blowout almost completely stabilized by bunch-grasses, especially *Leptoloma cognatum*.

PLATE X.

Fig. 1. Extensive tract of blowsand in the Oquawka area near Keithsburg.

Fig. 2. Development of the *Stenophyllus* association in a shallow blowout, Hanover area. The conspicuous erect plants are *Oenothera rhombipetala*.

PLATE XI.

Fig. 1. Development of the *Stenophyllus* association in a shallow blowout in the Hanover area. The conspicuous erect plants are *Oenothera rhombipetala*.

Fig. 2. Blowout in the Oquawka area. Stabilization is beginning, as shown by the persistence of the grasses at the base of the windward slope, the conspicuous plants of *Lespedeza captata*, patches of moss, and by the thicket of *Populus deltoides* in the background, at the left.

PLATE XII.

Fig. 1. Contact of the *Polytrichum* association with bare blowsand.

Fig. 2. Contact of the *Polytrichum* (see foreground) and bunch-grass associations.

PLATE XIII.

Fig. 1. Pond "*E*," in a depression between dunes in the Dixon area, showing the zones of vegetation.

Fig. 2. Invasion of the bunch-grass by the black oak association. Hanover area.

PLATE XIV.

Fig. 1. Black oak association, Oquawka area. Typical habitat of *Synthyris Bullii*.

Fig. 2. Typical opening in the black oak association, Oquawka area, with *Tephrosia virginiana*, *Monarda punctata*, *Opuntia Rafinesquii*, etc.

PLATE XV.

Fig. 1. Characteristic growth of *Pteris aquilina* near the margin of the black oak association, Winnebago area.

Fig. 2. Hillside in the Winnebago area, showing the transition from the black oak association on the upland (left) to the bur oak association in the lowland (right). The shrubbery is chiefly *Prunus virginiana*.

Fig. 1. Bur oak association, Winnebago area. *Rubus* sp. in the foreground, at the eft; *Pteris aquilina* conspicuous under the trees.

Fig. 2. Black oak association, Oquawka area. A few young vines of *Psedera* and *Celastrus* have appeared, indicating the beginning of the succession to the mixed forest.

PLATE XVII.

Fig. 1. Natural opening in the black oak association, Winnebago area, occupied by the bunch-grass association.

Fig. 2. Face of the river dune, Hanover area, showing the upper and middle slopes, separated by the outcrop of an old soil layer. The thicket association caps the dune in the background.

PLATE XVIII.

Fig. 1. Windward margin of the thickets on the river dune, Hanover area. The outermost tree at the left is a green ash. A small *Physalis heterophylla* association in the foreground, at the right.

Fig. 2. Dune thickets on the slope of the river dune, Hanover area. The exposed root system of the ash at the left indicates the migration of the dune

PLATE XIX.

Fig. 1. Associations on the river dune, Hanover area. In the right foreground, the deposit association, with a large bunch of *Panicum virgatum* and abundant *Aristida tuberculosa*; behind it, the *Smilacini* association; in the background the dune thickets, with a dense tangle of lianes.

Fig. 2. Margin of the dune thickets on the windward side of the river dune, Havana area. The effect of the migration of the dune is shown in the exposed roots. Forests of the Mississippi river flood-plain in the background.

PLATE XX.

Fig. 1. Destruction of the stabilized river-dune and its mesophytic vegetation by river erosion, and the reversion of the vegetation to the pioneer blowsand association. Oquawka area.

Fig. 2 Destruction of the mesophytic vegeta·ion of the river dune by river erosion, showing the coherent surface-layer of sand, and the sliding masses.